MIGRATION ECOLOGY OF SABINE'S GULLS (*Xema sabini*) FROM THE CANADIAN HIGH ARCTIC

by

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ABSTRACT

Sabine's gulls are the only Arctic gulls that undertake trans-equatorial migrations between their breeding grounds and offshore wintering areas. I used light-based archival geolocation devices (n = 36) to track Sabine's gulls from one of their northernmost breeding colonies, on Nasaruvaalik Island in the Canadian High Arctic, to their wintering sites in the Southern Hemisphere. I discovered that birds from Nasaruvaalik Island migrate to both the Pacific and Atlantic wintering areas this species is known to use, with the majority of birds migrating to a restricted area in the Humboldt Current off the coast of Peru and a small portion of the birds migrating to an area in the Benguela Current off the coast of South Africa. I characterized the routes, timing, and distance of Pacific wintering Sabine's gulls. Analysis of the movements of these individuals revealed that Sabine's gulls exploit highly localized areas of elevated marine productivity along a migration route of more than 28,000 km. I identified the Juan de Fuca Eddy off the southwest coast of Vancouver Island, British Columbia as a critically important foraging area during both north and southbound migration. I also describe the non-stop overland crossing by some birds between the Pacific and Arctic Oceans during northbound migration.

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1. Introduction and Overview

1.1 Thesis Background

Migration ecology

The study of animal migration provides insights into patterns of resource abundance, migratory corridors, foraging behaviour, and population ecology. While widespread across animal taxa, migration is particularly evident and well developed in birds that move between breeding and non-breeding areas (Webster et al. 2002). The drive to find food, both to provision chicks during the breeding season and to survive during the non-breeding season, is the strongest force influencing migration behaviour (Alerstam et al. 2003), and therefore occurs in association with, and in response to, seasonal changes in food availability (Newton 2010). Individuals exploit seasonal peaks and avoid seasonal depressions in resource abundance (Alerstam et al. 2003), resulting from the alternation of warm and cold seasons at high latitudes, or of wet and dry seasons in the tropics (Newton 2010). To understand the biology and ecology of migratory birds, it is first necessary to understand the relative importance of events occurring during both the breeding and non-breeding parts of the annual cycle of birds (Robinson et al. 2010, Webster et al. 2002).

Migratory connectivity is the extent to which individuals from the same breeding population overlap during the winter, and vice versa (Webster et al. 2002). The degree of connectivity ranges on a scale from weak to strong, and has a varying effect on the overall ecology of a species. Populations exhibiting strong migratory connectivity are

predicted to be more vulnerable to habitat changes or anthropogenic threats (e.g. González-Solís et al. 2007), while populations with weak or flexible connectivity may be buffered from threats in a particular area (e.g. Dias et al. 2011, Kopp et al. 2011). Ultimately, the most important factor in determining how migratory connectivity may affect overall survival is the extent to which specific threats during one part of the annual cycle are likely to affect the population at large (Marra et al. 1998).

Use of geolocators to study bird migration

Due to the inherent difficulties in following highly mobile individuals, there continue to be large gaps in our understanding of many aspects of migratory behaviour in birds. Fundamental knowledge such as the breeding and wintering ranges of some species is still lacking (Robinson et al. 2010), and the migratory connectivity of most bird species, particularly smaller species and those that spend the majority of time in remote or inaccessible areas remains poorly understood (Webster et al. 2002).

Early studies of migratory behaviour relied on observational surveys (McLaren 1982, Spear & Ainley 1999), mark-recapture (Pradel et al. 1997, Yong et al. 1998), radar observations (Biebach et al. 2000) radio telemetry (Aborn & Moore 1997, Iverson & Esler 2006, Plissner et al. 2000) or laboratory experiments (Marra et al. 1998, Phillips et al. 2009). Considerable advances in remote-sensing technologies over the last two decades have changed the way we study bird migration, providing opportunities to track individual birds with great precision and accuracy (Bridge et al. 2011, Burger & Shaffer 2008, Fiedler 2009). This new wave of migration research has offered extraordinary

insights into foraging behaviour (McKnight et al. 2013), energy requirements (Fort et al. 2013b), long-distance movements (Gill et al. 2008, Kopp et al. 2011), habitat associations (González-Solís et al. 2007), and risks associated with anthropogenic activities during the non-breeding season (Fort et al. 2013a, Montevecchi et al. 2012).

Geolocators are currently one of the most widely used tools to track birds, and are among the smallest and least expensive tracking devices available (Bridge et al. 2013). Geolocators continuously log ambient light intensity and time, and the records are used to determine time of sunrise and sunset. Latitude is calculated from day length, and longitude from the time of solar noon (Fiedler 2009). More sophisticated devices also store sea-surface temperature (SST), wet-dry cycles, dive depths, and altitude data. Unlike transmitting devices, geolocators must be recovered in order to download the data and therefore the tagged bird must be recaptured. Geolocators have revealed previously unknown migration patterns of many species (Åkesson et al. 2012, Rodríguez et al. 2009a, Salewski et al. 2013), as well as spectacular long distance migrations of smaller seabirds (Egevang et al. 2010, Fijn et al. 2013, Guilford et al. 2009), shorebirds (Johnson et al. 2012, Niles et al. 2010) and passerines (Stutchbury et al. 2009, Tøttrup et al. 2012). Although geolocators are widely recognized as one of the most reliable and least invasive methods to track individual birds, they also have several disadvantages, predominantly the relatively low accuracy of positional estimates compared with other methods such as satellite tags (Bridge et al. 2011). Light-based latitude estimates are prone to error, especially during equinox periods when day length is similar around the globe (Hill 1994), when birds are at high latitudes and experiencing continuous daylight (Egevang 2010), and at low latitudes when differences between day and night are less pronounced

(Shaffer et al. 2005). Latitudinal errors are also increased during the breeding season when tags are often shaded by birds sitting on nests (Ekstrom 2004), or when significant daily movements undertaken between sunrise and sunset increase or decrease perceived day length (Ekstrom 2004, Hill 1994). The mean error of filtered location estimates from geolocators deployed on seabirds ranges from 186 ± 114 km (Phillips et al. 2004) to 400 ± 298 km (Shaffer et al. 2005). SST data from satellites can be matched to tag data to improve estimates of latitude, particularly when there is definite north-south SST gradient (decreased error in Shaffer's 2005 study to 202 ± 171 km). With the continued development of processing algorithms (Ekstrom 2004, 2007) and techniques to improve the accuracy of location estimates (Lam et al. 2008, Shaffer et al. 2005, Teo et al. 2004), geolocators are quickly proving to be an invaluable tool to study migration routes and habitat use of a wide range of bird species.

While there are obvious benefits to using geolocators to study bird migration, the effects of tagging on individual birds must also be considered. Seabirds in particular may suffer because tags may affect both aerodynamic as well as hydrodynamic performance (Vandenabeele et al. 2012). Early studies that examined effects of tag deployment on seabirds focused on foraging behaviour, particularly hydrodynamic drag in diving species like penguins (Culik et al. 1994). Since then, many studies on the behaviour of tagged birds have revealed a variety of adverse effects (Barron et al. 2010). Direct effects, such as increased energy expenditure (Vandenabeele et al. 2012), decreased breeding success (Ackerman et al. 2004, Rodríguez et al. 2009b), reduced flight range (Navarro & González-Solís 2006, Passos et al. 2010), increased duration of foraging trips (Ballard et al. 2010, Hamel et al. 2004), decreased nest attendance (Soehle et al. 2000), and reduced

breeding site fidelity and colony attendance (Robinson & Jones 2014) have all been documented as a result of tagging in some seabirds. Indirect effects such as reduced parental investment causing a reduction in body size of chicks (Adams et al. 2009, Robinson & Jones 2014, Sæther et al. 1993) or mate compensation, in which mates of tagged birds increased chick provisioning and offspring attendance to compensate for poor performance of their tagged partner (Paredes et al. 2005) have also been noted. The sensitivity of birds to tagging disturbance varies considerably with transmitter load, and the negative effects associated with the attachment of tracking devices to birds may be reduced as tags become smaller and lighter (Phillips et al. 2003).

Ultimately, inter-species variation of tag deployment is great and effects must therefore be assessed on a case by case basis (Casper 2009). Vandenabeele et al. (2012) suggested that tag effects are likely to be strongest in seabirds with high wing loading and energetically expensive flapping flight like cormorants (Phalacrocoracidae) and Auks (Alcidae), but much lower in birds with a low cost flapping flight mode. This would place my study species – Sabine's gull (*Xema sabini*) – in a relatively low risk taxon for tag effect.

1.2 Sabine's Gull (*Xema sabini*)

History and taxonomy

The type specimen of the Sabine's gull (*Xema sabini*) was collected in 1818 by Edward Sabine, a naturalist onboard the *Isabella*, during an expedition to explore Baffin Bay in hopes of discovering a Northwest Passage (Mlikovsky 2012). Joseph Sabine (Edward's

brother) named and described the new species *Larus sabini* in Anals of Philosophy in 1819 (Anonymous), and the genus *Xema* was later authored by Ross (1819).

The Sabine's gull is phylogenetically unique, belonging to the single-species genus *Xema* (Crochet & Bonhomme 2000). Previously thought to be most closely related to the swallow-tailed gull **(***Creagrus furcatus*) based on morphological similarities (Chu 1998, Dwight 1925, Moynihan 1959), *X. sabini* was identified as a sister taxon to the ivory gull (*Pagophila eburnea*) based on a molecular phylogeny (Crochet & Bonhomme 2000), despite dramatic differences in plumage and morphology. Unlike the contrasted plumage of the Sabine's gull, the ivory gull shows an entirely white plumage which is thought to be a consequence of their year-round Arctic distribution (versus low latitude pelagic) (Crochet & Bonhomme 2000). It is thought that these species differentiated c. 2 million years ago (Crochet & Bonhomme 2000) in the High Arctic rather than colonizing the Arctic after differentiation (Day et al. 2001).

Distinguishing characteristics and behaviour

The Sabine's gull is a small gull (c. 190 g), unique in morphology and behaviour (Bent 1921, Brown & Jones 1967). Adult birds in breeding plumage are distinctive, most notably for their dark grey hood separated from a white neck by a black collar, yellow-tipped black bill, slightly forked tail, and striking black, white, and grey upper wing pattern (Plate 1). They have long narrow wings and fly with deep wing strokes which gives them a buoyant, tern-like appearance in flight (Day et al. 2001).

Plate 1. Adult breeding plumage of the Sabine's gull (*Xema sabini*), showing distinctive upper wing pattern, dark grey head, and black bill with a yellow tip (photo by Mark Maftei).

In addition to their distinctive morphological features, Sabine's gulls also have a molt pattern that differs from that of most other gulls. In adult birds, remigial moult occurs after migration, which is the reverse of most gulls with the exception of other long distance migrants such as the Franklin's gull (*Larus pipixcan*) (Grant 1997). Sabine's gulls undergo a complete moult in the spring, before starting northbound migration (Grant 1997, Howell & Dunn 2007). Juvenile Sabine's gulls retain their plumage through fall migration, starting moult into first-winter plumage only after they arrive at or near their

wintering site (Grant 1997). This pattern of moult likely reflects the energetic costs of Sabine's gulls' long-distance migration (Stenhouse et al. 2001).

Sabine's gulls also exhibit some aberrant breeding behaviours, most notably distraction displays more similar to shorebirds or jaegers than gulls (Stenhouse et al. 2005), and relocation of chicks to post-hatching territories (Forchhammer & Maagaard 1991, Stenhouse et al. 2001). In addition, they are the only Arctic gull to undergo trans-equatorial migration (Day et al. 2001).

Breeding range and habitat

Sabine's gulls breed across a circumpolar range, extending from Low Arctic taiga to High Arctic tundra (Figure 1-1). In North America, their breeding range extends from coastal Alaska across Arctic Canada and central High Arctic islands east to northern Hudson Bay and southwest Baffin Island (Figure 1-1). Outside North America, Sabine's gulls breed in the High Arctic zones of Greenland, Spitsbergen, and eastern Russia (Figure 1-1).

Sabine's gulls nest in single pairs, scattered groups, or within larger colonies, often in association with Arctic terns (*Sterna paradisaea*) (Blomqvist & Elander 1981, Day et al. 2001). In the Low Arctic, Sabine's gulls nest in low-lying, coastal salt marsh tundra (Brown & Jones 1967, Day et al. 2001, Stenhouse et al. 2001). In the High Arctic, they nest on small gravel islands, in low-lying areas sparsely covered in vegetation (Forchhammer & Maagaard 1991, Mallory et al. 2012). Breeding sites are typically near tidal ponds and lakes, freshwater rivers or lakes, or polynyas (Day et al. 2001).

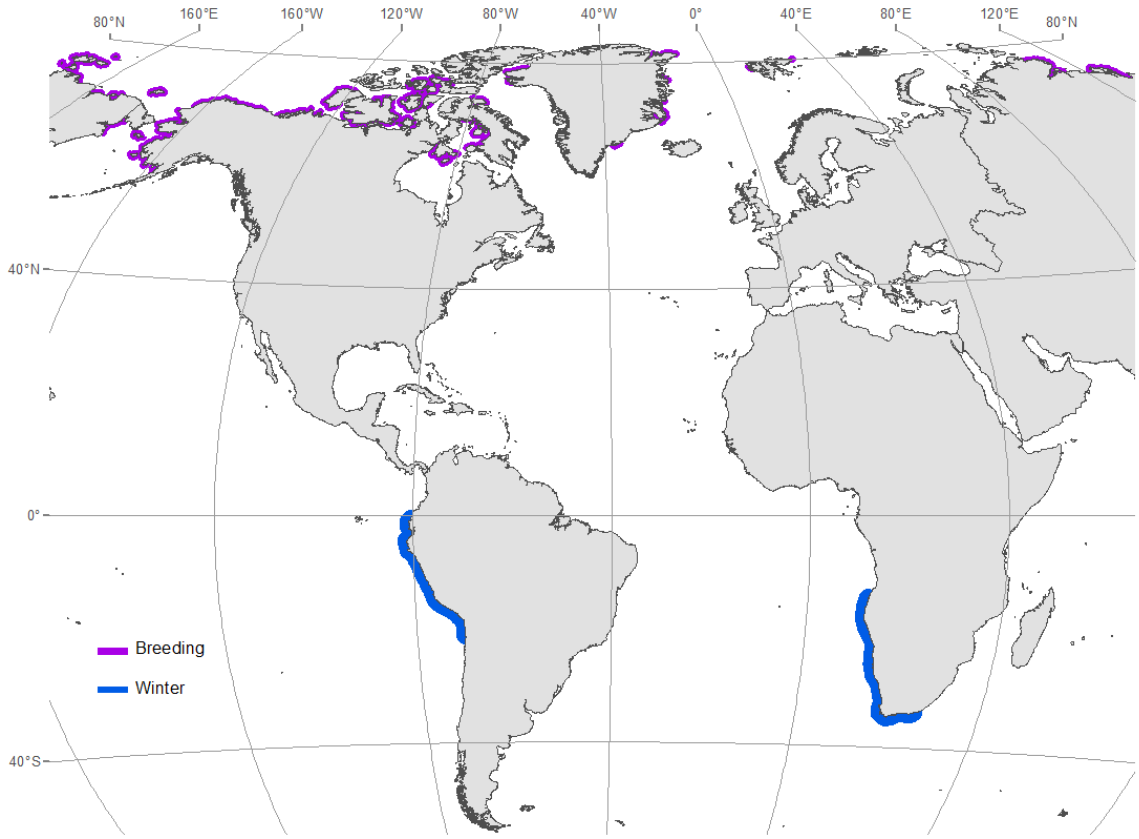

Figure 1-1. Distribution of Sabine's gull (*Xema sabini*) showing circumpolar breeding range and winter range in the Southern hemisphere (adapted from text in Day et al. 2001).

Winter range and habitat

Sabine's gulls winter within the two major coastal upwelling systems in the Southern hemisphere; within the Humboldt Current off the coast of Peru in the Pacific, and in the Benguela Current off the coast of Namibia and South Africa in the Atlantic (Figure 1-1; Day et al. 2001).

In the Pacific, the winter range of the Sabine's gull has been determined from at-sea surveys and coastal observations (Chapman 1969, Duffy 1983, Plenge et al. 1990,

Post 1971), which indicate that birds are primarily found in areas of intense coastal upwelling off the coast of Peru, occasionally venturing South into Chilean waters (Chapman 1969, Post 1971), and North to waters off the coasts of Ecuador and Columbia. These sightings are likely of gulls still on migration (Chapman 1969, Olsen & Larsson 2004). The most extensive surveys in the Pacific were conducted by Chapman (1969), who showed peak numbers of Sabine's gulls within the Humboldt Current from December to February (no voyages occurred in March). The highest concentrations of birds were seen less than 20 km offshore, between 15-18°S, with a smaller peak of concentration in near shore waters between 6-8°S (Chapman 1969).

The winter range of the Sabine's gull in the Atlantic was only recently described by Stenhouse et al. (2012) using geolocators (n = 8) deployed on birds from the small population breeding in Eastern Greenland. Birds from this study site were found to winter primarily off the coasts of Namibia and South Africa, between 20° and 30°S. At-sea surveys and incidental sightings in the Atlantic suggest a broader Atlantic wintering range, which includes the waters off southern Angola to the north, as well has low numbers wintering in the Indian Ocean within the Agulhas Current off the southern coast of South Africa to the southeast (Lambert 1972, Urban et al. 1986, Zoutendyk 1965, 1968).

Migratory behaviour

Flying between their Arctic breeding range to offshore wintering sites in the Southern hemisphere, Sabine's gulls apparently undertake the longest known migration of any gull

(Stenhouse et al. 2012). Sabine's gulls are highly pelagic during the non-breeding season, and move rapidly from their Arctic breeding sites to towards lower latitudes for the winter. The migration behaviour of Sabine's gulls is poorly studied, although birds have been observed flying in flocks that range from small (1-5 individuals) to large (1000+ individuals), low to the water, stopping frequently to feed (Day et al. 2001). Sabine's gulls have often been seen flying in mixed flocks or in close association with Arctic terns (Lambert 1972). Sabine's gulls are mostly pelagic during migration and have been recorded flying along the shoreline to at least 200 km offshore, most numerous over the shelf break (Briggs et al. 1987, Morgan et al. 1991). When seen during migration, Sabine's gulls appear to fly leisurely, stopping for hours to gather around fishing vessels, resting on ice edges, or swimming around foraging in the surface waters (Lambert 1972). It is possible that this unhurried flight behaviour occurs only during the day, during which birds rest and feed, and Sabine's gulls migrate mostly at night (Lambert 1972), however this has not been confirmed. Migration was previously suggested to be more prolonged during fall (northbound) and rapid in the spring (northbound) (Briggs et al. 1987, Vermeer et al. 1989).

Routes and timing of migration

Sabine's gulls breeding in Russia, Alaska, and western Canada are thought to migrate from the Gulf of Alaska, along the western coasts of North and South America to winter in the Pacific off the coast of Peru (Day et al. 2001). Birds from eastern Canada are thought to cross Davis Strait joining migrants from Greenland, then crossing the North

Atlantic to follow the western coasts of Europe and Africa to winter in the Atlantic off the coast of South Africa (Day et al. 2001). After breeding, Sabine's gulls form large flocks near shore and feed in the water or on beaches (Bent 1921, Stenhouse et al. 2001). Adults purportedly leave the breeding areas before newly fledged young (Bent 1921, Cramp et al. 1983). Failed breeders may begin fall migration as early as July (Harrison 1985).

Pacific migrants are observed in northern and western Alaska from late August to early September (Day et al. 2001) and are observed in southwestern Alaska and the Gulf of Alaska as late as early November (Gould et al. 1982). Sabine's gull abundance peaks off the southwest coast of Vancouver Island in late August to early September (Morgan et al. 1991, Vermeer et al. 1989), with concentrations observed over Swiftsure Bank and La Perouse Bank (Morgan et al. 1991). Morgan et al. (1991) suggested this area is an important feeding area for Sabine's gulls during fall migration. Along the U.S. coast, fall migration occurs off the coasts of Washington and Oregon from late August to September (Day et al. 2001), and off California from August to October (Briggs et al. 1987). Sabine's gulls arrive at their wintering grounds off the coast of Peru between August and December (Chapman 1969, Duffy 1981). Spring migration begins off the coast of Peru between February and April (Blake 1977, Chapman 1969), and birds have been observed on migration off California beginning late April until late May (Briggs et al. 1987) and off British Columbia from April to early June (Campbell 1990, Morgan et al. 1991). Sabine's gulls are first noted arriving on Alaskan breeding grounds between late April and early June and on Canadian Arctic breeding grounds in early to late June (Day et al. 2001).

Atlantic migrants show peak movement leaving the Arctic from August to mid-September (Day et al. 2001), occasionally as late as October (Brown et al. 1975, Salomonsen 1951). Birds concentrate in the Bay of Biscay and Iberian Sea, off the coasts of France, Spain and Portugal in mid-August to mid-September (Lambert 1972, Stenhouse et al. 2012). It is also likely that a portion of the Atlantic population follows the eastern coast of Canada and the U.S. south before crossing the Atlantic to the wintering site indicated by a number of sightings during fall migration (see Day et al. 2001, Lambert 1972). Sabine's gulls continue south and are obsered along the west coast of Africa between late August and November (Cramp et al. 1983, Stenhouse et al. 2012), with earliest arrivals to the wintering area off the coast of South Africa in late September (Lambert 1972), peaking between October and November (Stenhouse et al. 2012). Atlantic Sabine's gulls remain in the wintering area until spring, with birds beginning spring migration between March and early May (Lambert 1972, Stenhouse et al. 2012). Birds are observed off northwest Africa between mid-March and June, peaking in early May (Stenhouse et al. 2012), spending two to three weeks staging off the coast of Morocco before moving north (Stenhouse et al. 2012). Sabine's gulls are obesrved off the coasts of Newfoundland and Labrador as well as Greenland between late May and early June (Lambert 1972). Atlantic migrants arrive in to their Arctic breeding grounds between late May and mid-June (Lambert 1972, Stenhouse et al. 2001).

It has been suggested that some Sabine's gulls may travel overland during portions of either fall of spring migration (Day et al. 2001, Lambert 1972, Portenko 1989). Lambert (1972) hypothesized that fall migration of birds breeding in the Canadian Arctic may involve overland movement across northeastern Canada and the United States

to the Atlantic, based on multiple sightings of Sabine's gulls in the interior of the U.S., Great Lakes, and upper Gulf of St. Lawrence during September (Cramp et al. 1983, Lambert 1972). The scarcity of inland records in the fall, and the fact that these consist almost entirely of juveniles (or possibly lost vagrants) might suggest a mainly marine (not overland) migration pathway in the fall, especially around eastern North America. During spring migration, Lambert (1972) also suggested that birds may fly overland from the North American east coast to Hudson Bay, based on a few inland observations of adults in spring in this area (see Day et al. 2001). In contrast, there have been spring records of Sabine's gulls in the interior of northwestern Canada and the U.S. (see Day et al. 2001), which may be attributed to a common overland route from the Pacific to the Arctic, however concrete evidence for this as a regular migration route involving a substantial proportion of the population has not been previously confirmed. On Wrangel Island in Russia, Sabine's gulls have been seen flying directly across the island through high mountain passes (Portenko 1989).

First year birds are thought to stay south of the breeding grounds during the first summer (Cramp et al. 1983, Urban et al. 1986), however it is entirely unknown what areas they use during this time. They have been occasionally seen in higher latitudes, off the coast of Labrador, near Southampton Island, NU, and off the coast of Maine, all during mid-July (Lambert 1972), suggesting substantial numbers may summer in the northern hemisphere (Day et al. 2001).

Foraging behaviour

Sabine's gulls feed on terrestrial and freshwater invertebrates, marine zooplankton, and small fish during the breeding season (Abraham & Ankney 1984, Brown & Jones 1967, Stenhouse et al. 2012). The diet of Sabine's gulls during the non-breeding season is poorly studied, although birds clearly target areas of high and consistent marine productivity within large coastal upwelling zones. Sabine's gull forage offshore, and are often found along lines of foamy, plankton-rich water (caused by Langmuir circulation) characteristic of productive upwelling areas (Chapman 1969). Sabine's gulls forage primarily by pursuit plunging, as well as surface feeding, pattering, and scavenging behind fishing vessels (Abrams 1983, Duffy 1983, 1989). They are known to feed on zooplankton swarms in the Humboldt Current (Duffy 1983), and on zooplankton swarms, fish schools, and over foraging fur seals in the Benguela Current (Duffy 1989). Attraction to fishing vessels and scavenging of fishery discards has also been confirmed for Sabine's gulls (Duffy 1983, 1989; Valeiras 2003).

Population and Conservation

There are limited data on Sabine's gull populations and trends due to a lack of comprehensive surveys, which would be in any case impractical if not impossible for a species which nests in low density across a vast and remote Arctic range (Day et al. 2001).

The global population estimate for Sabine's gull is c. 330,000 - 700,000 (IUCN 2014). In Canada, the estimated breeding population is 25,000 - 50,000 (Environment

Canada 2011). Foxe Basin is considered to contain the majority of breeding birds in Canada, with estimates of c. 25,000 concentrated on Prince Charles Island and Air Force Island (Johnston & Pepper 2009), and c. 26,000 in all of Foxe Basin and northern Hudson Bay (Gaston et al. 2012). Surveys of Banks and Victoria Island in the eastern Canadian Arctic yielded estimates of c. 1800 birds in 1993-1994 (Cornish & Dickson 1996), and c. 450 birds in 2005 (Raven & Dickson 2006). In the northernmost part of their Canadian breeding range within Queens Channel, there is an estimated population of c. 300 birds (Maftei et al. 2015 in press). Estimates of the Russian breeding population are highly variable, and range from c. 2000 individuals (Kondratiev 1991) to c. 100-10,000 birds (Brazil 2009). A small population of 200-1000 Sabine's gulls breeds in Greenland (Status and Conservation of the World's Seabirds 1986). Scattered pairs of Sabine's gulls also occasionally breed on Spitsbergen (Cramp et al. 1983). The only non-breeding population data are derived from at-sea surveys within the Pacific wintering area, with estimates of c. 100,000 individuals (Shuntov 1998). The Atlantic wintering population has not been estimated.

Sabine's gulls are considered a species of Least Concern (LC) globally (IUCN 2014), and are not at risk in North America due to significant populations (Day et al. 2001). Sabine's gulls are listed as near threatened (NT) in Greenland (Boertmann 2007), due to the small population size. Despite their patchy distribution and low numbers (Kondratyev et al. 2000), Sabine's gulls are not included in the Red Book of Russia (Andronov 2000).

On account of the general inaccessibility of their breeding range, Sabine's gulls are thought to be relatively unaffected by anthropogenic disturbance during the breeding

season, although human disturbance has been reported to decrease hatching success in Greenland (Forchhammer & Maagaard 1991) and disturbance from herds of reindeer decreased nesting populations in Russia (Kondratiev 1991). Non-breeding threats have not been quantified, however their known wintering and stopover sites in highly productive marine areas overlap with major commercial fisheries, shipping, and tourism, which may affect food availability, increase exposure to contaminants, and/or cause physical disturbance (Day et al. 2001, Stenhouse et al. 2012). This concern is somewhat mitigated by the birds' offshore distribution, that limits contact with most human activity.

1.3 Thesis Objectives

Most research on Sabine's gulls has focused on breeding biology and behaviour (e.g. Abraham 1986, Brown & Jones 1967, Kondratyev & Kondratyeva 1984, Mallory et al. 2012, Stenhouse et al. 2001), while most aspects of the non-breeding ecology of this species are as yet unknown due to the difficulty of research on such a highly mobile pelagic species. One of the most significant gaps in our understanding of the ecology of Sabine's gulls is the lack of conclusive evidence identifying migration routes and wintering sites used by various breeding populations (Day et al. 2001). Current information pertaining to the migratory movements of Sabine's gulls in the Pacific is largely derived from incidental sightings, and the huge distances between known breeding and wintering areas make it impossible to ascertain to what extent birds from different parts of the circumpolar breeding range of the species use different wintering areas.

Furthermore, beyond incidental sightings, virtually nothing is known about their stopover and winter habitat use in the Pacific.

The goal of my thesis is to examine the movement and distribution of Sabine's gulls from a breeding site in the Canadian High Arctic. My research addresses five important questions: (1) Where do Sabine's gulls breeding in the Canadian High Arctic spend the winter? (2) What degree of migratory connectivity does the breeding population show (i.e., is there variation in winter destinations)? (3) How and when does Sabine's gull migration take place (what are the routes taken, timing of movements and distance travelled)? (4) Do Sabine's gulls show sex-related variation in migration timing similar to many other seabird species? (5) What stopover and wintering areas are used by Sabine's gulls during the non-breeding season, and are the areas productive coastal upwelling areas, similar to areas confirmed by Stenhouse et al. (2012)?

1.4 Chapter Outlines

In Chapter One (this chapter), I introduce background information relevant to my thesis, a detailed species account of the Sabine's gull, as well as my thesis objectives. In Chapter Two, I use geolocators to track Sabine's gulls from a breeding site in the Canadian High Arctic to identify their wintering destinations (Pacific or Atlantic) and examine the variation that is found within the breeding population. In Chapter Three, I examine the Pacific migration of Sabine's gulls in detail, describing the routes taken, timing of migration, distance and speed travelled, as well as variation between the sexes. I identify the critical stopover areas used and define the range of the Pacific wintering area used by

Sabine's gulls from my study site. Finally, in Chapter Four, I summarize the results of my research, discuss conservation implications, and suggest future research objectives.

1.5 Statement of Authorship

Thesis author

I was principally responsible for the research proposal and study design, the practical aspects of the research, the data analysis, and the manuscript preparation.

Co-authorship statement

This research was co-supervised by Dr. Mark Mallory (Acadia University) and Dr. Ian Jones (Memorial University). Mark Mallory provided research supervision and was responsible for securing funding and support for most of my field research, including travel, field supplies, and permits. He is responsible for the original research idea, and funded and carried out the field work to deploy the original geolocators in 2008 as well as the first round of geolocators in 2010. He was involved in discussions of study design and data analysis, and provided revisions on my thesis. Dr. Ian Jones provided academic supervision throughout and personal support during the second year of my degree. He was involved in discussions regarding study design and data analysis, and provided revisions on my thesis. Mark Maftei contributed significantly to the practical aspects of the research, assisting me in the field deploying and recovering geolocators. He was primarily responsible for securing a large grant, which purchased the majority of

geolocators as well as important field supplies. He was involved in discussions about study design and data analysis throughout the entire process and provided feedback and revisions on my thesis.

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2. Breeding on the Divide: Sabine's Gulls (*Xema sabini*) from the Canadian High Arctic Migrate to both Pacific and Atlantic Wintering Sites

2.1 Abstract

The world's Arctic latitudes are some of the most recently colonized by birds, and a growing understanding of the migratory connectivity of circumpolar species offers unique insights into the mechanisms of range expansion and speciation. Longitudinal migratory divides within the Nearctic are known to exist for many breeding birds, however for most taxa it is unclear where the boundaries lie, and to what extent these affect the connectivity of species breeding across their ranges. Sabine's gulls (*Xema sabini*) have a patchy but circumpolar breeding distribution and breed across the Nearctic from western Alaska to Eastern Greenland. Sabine's gulls are known to winter in two geographically distinct areas in different ocean basins separated by thousands of kilometers, but that are ecologically similar: the Humboldt Current off the coast of Peru, and the Benguela Current off the coast of South Africa. Despite considerable speculation, it has never been confirmed where the migratory divide for this species lies in the Nearctic, and to what extent gaps in the non-contiguous circumpolar breeding range may reflect segregation to different wintering areas. Here, I provide quantitative evidence that confirms that Sabine's gulls from a single colony in the central Canadian High Arctic disperse to both the Pacific and Atlantic during the non-breeding season. This suggests that a dividing line between different wintering populations of this species may exist in the Central Canadian High Arctic, and that migratory connectivity of Nearctic Sabine's gulls breeding near to or within the migratory divide may be more diffuse than previously assumed. My research

leads to a variety of ecological, behavioural and genetic questions about how the extreme long-distance migration pathways of this remarkable bird are determined, with general theoretical implications for our understanding of migratory behaviour of high latitude species.

2.2 Introduction

Determining the extent to which breeding populations overlap during the non-breeding season (i.e. migratory connectivity; Webster et al. 2002) is essential for interpreting ecological and evolutionary patterns of migratory species (Webster & Marra 2005). Strong or high migratory connectivity occurs when most individuals from one breeding population migrate to the same non-breeding area (Hedd et al. 2012), while weak or diffuse migratory connectivity occurs when individuals from a one breeding population migrate to several different non-breeding areas (e.g. Dias et al. 2011, Kopp et al. 2011, Webster et al. 2002). The strength of migratory connectivity has important conservation implications; for example events that occur at a species wintering site (e.g., habitat alteration) may influence subsequent events such as reproductive success at the breeding site at the individual level and, ultimately, the population level (Marra et al. 2011, Rockwell et al. 2012).

A complete division between breeding populations in which individuals from one breeding population move to different wintering sites (or vice versa) is common in many migratory bird species (Gudmundsson et al. 2002, Helbig 1996, Macdonald et al. 2012). These population level differences in migration patterns may evolve slowly, driven by

physical factors such as glacial events or the alteration of favourable habitat (Kraaijeveld & Nieboer 2000), or biological factors such as distribution of resources, energetic costs of migration, or competition between breeding populations (Alerstam 2011, Alerstam et al. 2003).

For many Palearctic migratory birds, there is a distinct migratory divide (defined as a narrow region of contact between populations with divergent migratory directions; Mayr 1942) at 100°E along the Taymyr Peninsula in Russia, which forms the most northerly continental barrier to east-west migration, and lies roughly halfway between suitable wintering habitat in the Atlantic and Pacific regions (Alerstam & Gudmundsson 1999a). Exceptions to this migratory divide exist, such as the cross-hemisphere migration of the Northern Wheatear (*Oenanthe oenanthe*) from Alaskan breeding grounds west across the Palearactic to winter in Eastern Africa (Bairlein et al. 2012).

Corresponding efforts to study migration patterns in the Nearctic have failed to find a consistent geographic divide between migratory bird species (Gudmundsson et al. 2002). Populations of most species of shorebirds appear to be divided in the western Arctic (Gratto-Trevor et al. 2012), while populations of some passerines (e.g. snow bunting) follow a divide in the east (e.g. Macdonald et al. 2012). Jaegers, terns, and gulls (Gudmundsson et al. 2002), as well as some duck species (Dickson 2012, Mehl et al. 2004, Mosbech et al. 2006) have sub-populations that migrate east and west out of the Nearctic, with no consistent shared boundary between species.

The Canadian High Arctic is a vast archipelago consisting of many terrestrial and marine habitats. The Arctic tundra system that is found within the archipelago is part of an nearly continuous area of relatively homogenous habitat that extends from the Nearctic

to the Palearctic (Henningsson & Alerstam 2008). Many breeding species can therefore occupy large or even circumpolar ranges, however these species typically consist of discrete populations that breed and winter in disjunct ranges with varying degrees of migratory connectivity (Henningsson & Alerstam 2008). The study of migration patterns in this geographic region is of particular interest for several reasons; (i) it is ecologically a very "young" area, having only become favourable as nesting habitat for birds since the last major ice age (Kraaijeveld & Nieboer 2000), (ii) it extends so far north of the Nearctic continental landmass that in its northern reaches it is physically an equally likely destination for migrants from the both the Nearctic and western Palearctic, and (iii) it extends from the North American continent symmetrically, so that its relative midpoint lies approximately equidistant from both the Atlantic and Pacific coasts (Gudmundsson et al. 2002). These three factors have resulted in the colonization of the High Arctic archipelago by migratory species from three source regions: Atlantic, Pacific and Palearctic (Bairlein et al. 2012, Gratto-Trevor et al. 2012, Mehl et al. 2004). Determining how species and populations are distributed through the Canadian High Arctic archipelago can help clarify the evolutionary process behind the migration patterns expressed by Arctic birds (Gudmundsson et al. 2002).

The Sabine's gull (*Xema sabini*) is a small gull which breeds across a patchy but circumpolar range (Day et al. 2001). It is highly pelagic in the non-breeding season, and spends the majority of its annual cycle in offshore waters (Stenhouse et al. 2012). All breeding populations are thought to migrate to either of two known wintering areas in major upwelling systems in the southern hemisphere (Blomqvist & Elander 1981, Stenhouse et al. 2012). The Pacific wintering population occupies a region within the

Humboldt Current off the coast of Peru (Chapman 1969), while the Atlantic wintering population occupies a region within the Benguela Current off the coast of South Africa and Namibia (Lambert 1972, Stenhouse et al. 2012). It is remains unclear how Sabine's gulls segregate between these two ecologically similar but extremely geographically disparate wintering areas, and the distribution of Atlantic and Pacific wintering birds at breeding colonies is unknown (Cramp et al. 1983, Day et al. 2001). Birds breeding in Siberia, Alaska, and the Western Canadian Arctic are thought to winter in the Pacific, while birds from breeding sites in the Eastern Canadian Arctic, Greenland, and Svalbard are thought to winter in the Atlantic (Blomqvist & Elander 1981). The migratory divide between Atlantic and Pacific wintering populations in the Palearctic is thought to lie along the Taymyr Peninsula (Alerstam & Gudmundsson 1999b), while the divide in the Nearctic is expected to lie somewhere in the central Canadian Arctic (Alerstam & Gudmundsson 1999a, Blomqvist & Elander 1981).

My study used geolocators to track Sabine's gulls breeding at a colony in the central Canadian High Arctic in order to determine their migratory inclination, which theoretically could be either to migrate west from the breeding grounds to winter within the Pacific, or east from the breeding grounds to winter in the Atlantic. Further, I aimed to interpret the revealed pattern of migration behaviour in relation to various hypotheses about how different Sabine's gull migration patterns across their Arctic range might be determined.

2.3 Methods

Study site

I conducted field research on Nasaruvaalik Island, Nunavut, (75.8˚ N, 96.3˚ W; Figure 2-1), between early June and late August over five years between 2008-2012. Nasaruvaalik Island is a small gravel island 1.4 km^2 in size, supporting a large and diverse colony of marine birds that forage in several nearby polynyas. The island is characteristic of the High Arctic tundra ecoregion (Olson et al. 2001) and has been previously described in detail (Mallory et al. 2012). Sabine's gulls are annual breeders, with the Nasaruvaalik Island colony size ranging from 16-31 breeding pairs over eight years of study, all of which nest in association with both Arctic terns (*Sterna paradisaea*) and Ross's gulls (*Rhodostethia rosea*) in two colonies at either end of the island. Sabine's gull philopatry at this site is high, based on capture-mark-resighting studies of colour marked birds (Davis et al. unpub.). Nesting habitat in the colonies consists of low gravel beach ridges interspersed with patches of moss and purple saxifrage (*Saxifraga oppositifolia*) and small, shallow ponds (Mallory et al. 2012).

Deployment and recovery of geolocators

I deployed 47 geolocators (44 LAT2900 and 3 LAT2500, Lotek Wireless, Canada) on 36 adult breeding Sabine gulls on Nasaruvallik Island over three years. In 2008, I deployed geolocators on three birds. In 2010, I deployed geolocators on 23 birds, one of which was previously tagged in 2008. In 2011, I deployed geolocators on 21 birds, 10 of which were tagged previously in 2010. In total, I deployed geolocators on 18 females and 18 males,

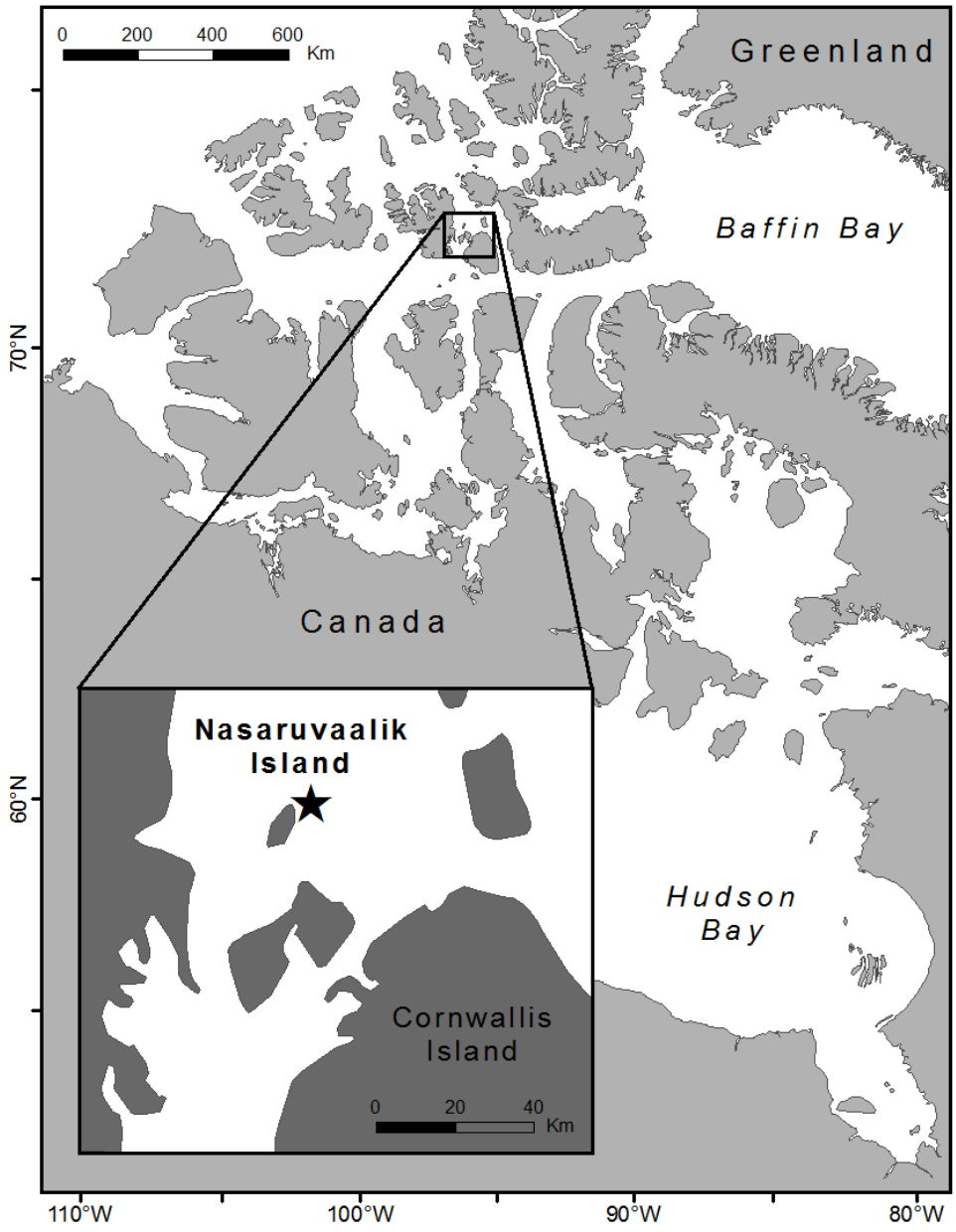

Figure 2-1. Location of the study site at Nasaruvaalik Island, Nunavut (75.8º N, 96.3º W), in the Canadian High Arctic (North Pole Lambert Azimuthal Equal Area projection).

11 of which (six males and five females) I tagged twice. I captured breeding Sabine's gulls with a spring-loaded bow net (Bub 1991) or a handheld CO_2 powered net gun (see Edwards & Gilchrist 2011 for details). I attached geolocators to Darvic tarsal bands with plastic cable ties (Plate 2), totaling 2.1g (LAT2900) and 3.8g (LAT2500), averaging 1.1% and 2.0% of adult body weight respectively. All tagged birds were also fitted with a numbered metal band and a unique combination of Darvic bands on the opposite leg (Plate 2). I determined the sex of tagged birds through an analysis of 2-3 drops of blood collected from the brachial vein (as described by Quintana et al. 2008). I recaptured tagged birds the following year to recover the geolocators (one unit was recovered after two years), and downloaded the data in LAT Viewer Studio© (Lotek Wireless, Canada).

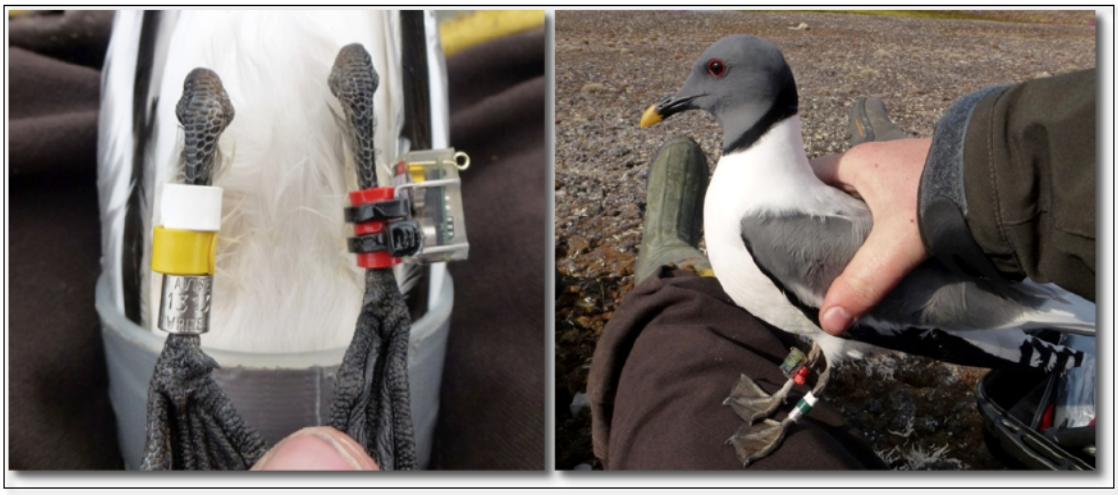

Plate 2. Captured Sabine's gull, showing geolocator (LAT2900) attached to a Darvic tarsal band with a numbered metal band and a unique combination of Darvic bands on the opposite leg.

Data processing

The geolocators used in this study estimated location once daily; latitude was estimated from the duration of daylight between sunset and sunrise, and longitude from the exact time of sunrise and sunset (Ekstrom 2004). The geolocators sampled sea-surface temperature (SST) when immersed for more than two consecutive samples (i.e. 120 s) and recorded the minimum daily value (°C) (Lotek Wireless 2010). To improve the accuracy of latitude estimates, I used SST correlation (LAT Viewer Studio©) based on the approach used by Shaffer et al. (2005), which allowed me to retain data around the equinoxes. I used 8-day composites of nighttime SST grids from the MODIS TERRA satellite in this study (http://whiteshark.stanford.edu/public/lotek_sst/, 4 km resolution), which are suitable for comparison to the tag values (Warnock 2010). I then filtered locations (Freitas 2012) to remove positions implying an unrealistic flight speed in Program R (R Core Team 2013). I assumed Sabine's gulls did not exceed a maximum velocity of 13.9 m/s (> 50 km/h sustained over a 48 h period) (Hedenström 1998). To further reduce the mean error in positions estimates, I smoothed each track using a moving weighted average (with a window size of three), whereby each smoothed position was the weighted average (in a 1:2:1 ratio) of the previous, current, and subsequent position (as per Fifield et al. 2014). Fixed start positions (at breeding colony) and positions that showed large daily movements (greater than 4° of longitude or 6° degrees of latitude) were not smoothed to avoid introducing positional errors (Phillips et al. 2004).

Analysis of movement data

I pooled all valid locations and generated kernel density estimations to represent the annual distribution of tracked birds (ESRI ArcGIS 10.1, search radius: 200 km, output cell size: 10 km). I created occupancy contours (25, 50, 75%) in Geospatial Modelling Environment (GME; Beyer 2012) to determine areas of high use throughout the annual cycle. I used the 50% occupancy contour generated around either one of the known wintering areas in the Southern Hemisphere (Day et al. 2001, Stenhouse et al. 2012) to set the boundary for the "wintering area". For the purpose of this study, I did not use positions that occurred after the wintering period (spring migration) in the remaining analysis (see Chapter 3 for full discussion of the annual migration of Pacific migrating Sabine's gulls).

I assigned positions to either "stopover" or "travel" categories with each bird initially defined to be in a stopover period (i.e. starting at the breeding site). I identified transition to a travel period when three or more positions (within a sliding window of five) showed movement more than 100 km/d. Similarly, I identified transition back to a stopover period when three or more positions failed to meet the distance criteria (less than 100 km/d) (method adapted from Fifield:2014bj and Gilg et al. 2013). Stopover periods were then examined for burst travel days, which occurred when birds travelled fast and far for 1-2 d, which would not trigger a transition to travel, however birds were clearly travelling to a new stopover area (Warnock 2010). These burst travel days were manually adjusted to reflect the travel behaviour.

Tracks were then split into two periods; fall migration and winter. Fall migration was defined as the period between departure from the breeding area (i.e., first "travel" location identified after breeding period) and arrival to the wintering area (i.e., first "stopover" location within the pre-defined wintering area) (as per Fifield:2014bj and Ramírez et al. 2013). For each wintering site (Pacific and Atlantic), I generated kernel density estimations (ESRI ArcGIS 10.1, search radius 200 km, output cell size 10 km) using winter locations, which I first transformed to an equal area projection appropriate for the site (South America Albers for Pacific and Africa Albers for Atlantic). To represent the distribution of birds at each wintering site, I created 25%, 50%, and 75% occupancy contours (GME; Beyer 2012).

I calculated great-circle distances between each pair of valid locations in Program R (R Core Team 2013), and subsequently calculated distance per day based on the number of days between locations. Travel distance (km) was defined as the distance travelled during fall migration not including movement during stopover periods, and travel speed (km/d) as the travel distance divided by the days travelled ("travel" days only) during fall migration (as per Fijn et al. 2013).

2.4 Results

Geolocator recovery and data details

I recovered 38 of 47 (81%) geolocators deployed on Nasaruvaalik Island. Four additional tagged birds were seen at the colony, but did not breed so I was unable to capture them, while one bird returned and successfully bred but had lost its geolocator prior to

resighting (92% of tags were re-sighted). The remaining four tagged birds (two pairs) did not return to the breeding site in either 2012 or 2013.

After filtering, my dataset contained 6,350 locations (91.7% valid), averaging 176 days per track. Twenty-eight geolocators tracked birds to their wintering site, while eight geolocators confirmed migration direction (Pacific or Atlantic) but failed before arrival to the wintering site. Two geolocators failed during the breeding season and were not included in the analysis (n = 36). Nine birds were tracked twice; therefore my data describes the movement of 27 individual birds.

Wintering sites used

Birds breeding on Nasauvaalik Island disperse to both the Atlantic and the Pacific during the non-breeding season (Figure 2-2-A). The majority of birds tracked (92.6%) migrated to the Pacific Ocean and wintered within the Humboldt Current off the coast of Peru (Figure 2-2-B). Two of the birds tracked (7.4%, both males) migrated east towards the Atlantic Ocean and wintered within the Benguela Current off the coast of Namibia and South Africa (Figure 2-2-C). Suprisingly, one pair of Sabine's gulls (confirmed mates for six seasons) tracked for two consequetive years spent both non-breeding seasons in different oceans (Figure 2-2-A; red and green tracks).

Sabine's gulls showed high wintering site fidelity; all nine birds that were tracked for two years wintered in the same area both years, including one Atlantic wintering bird.

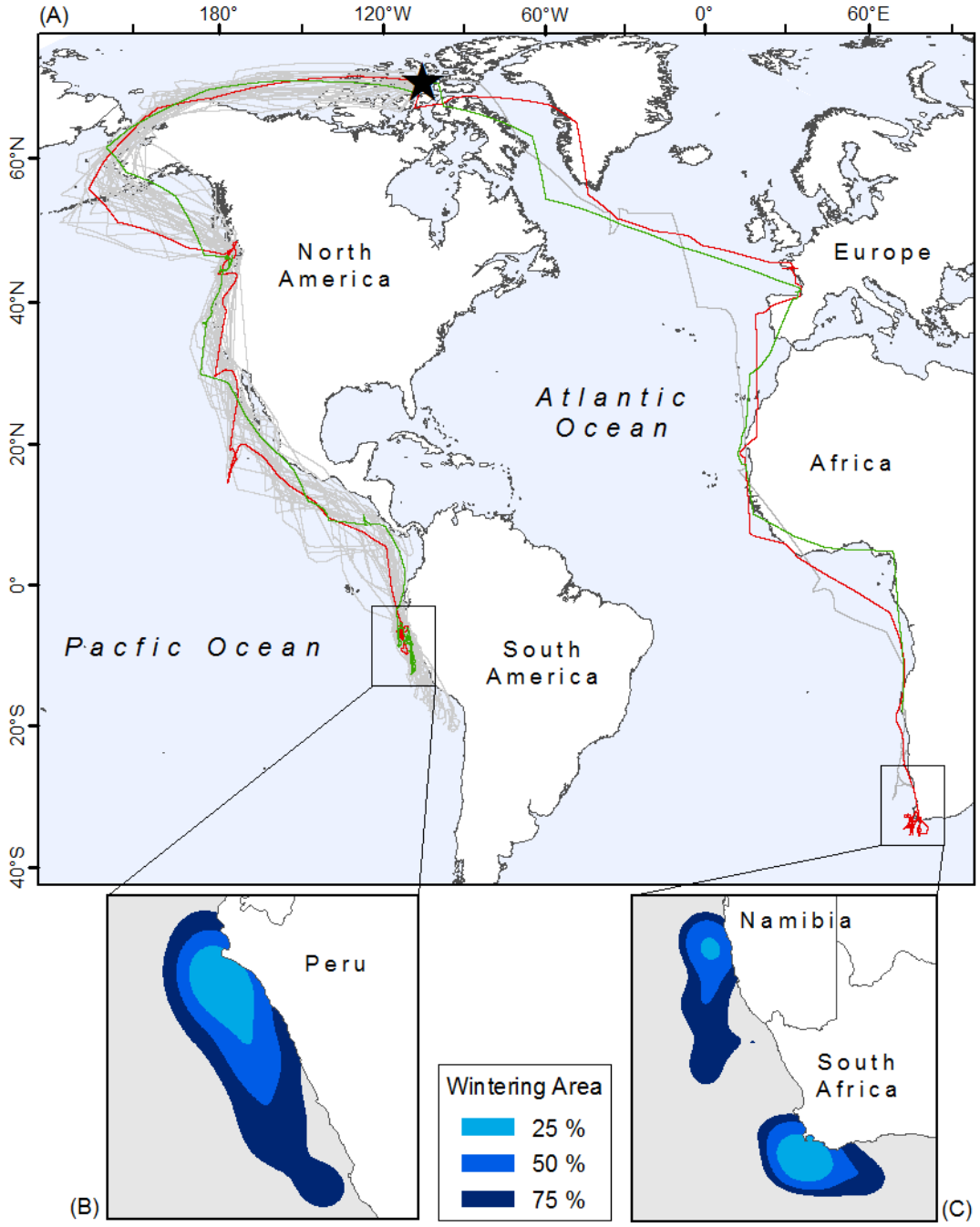

Figure 2-2. (A) Southbound migration of Sabine's gulls breeding at a site in the Central Canadian Arctic (black star), showing Atlantic tracks (*n* = 3) and Pacific tracks (*n* = 33). One breeding pair tracked for two consecutive years spent both non-breeding seasons in different oceans (red = 2010/11, green = 2011/12). (B) Pacific wintering area, with 25%, 50%, and 75% occupancy contours (*n* = 26). (C) Atlantic wintering area, with 25%, 50%, and 75% occupancy contours (*n* = 2).

Migration details

Sabine's gulls left the breeding site in late August and arrived at the wintering site in early November (Table 2-1). During fall migration, tagged birds travelled 14,578 km to the Pacific wintering site, and 14,615 km to the Atlantic wintering site, excluding movement during stopover periods (Table 2-1). Both Pacific and Atlantic birds spent 84 days migrating to the wintering site, flying at a speed of c. 350 km/day on travel days (Table 2-1). There was no significant difference in travel distance ($t_1 = 0.02$, $p > 0.5$) or travel speed ($t_8 = 0.41$, $p > 0.5$) between Pacific and Atlantic wintering populations.

Table 2-1. Fall migration details of Sabine's gulls (*Xema sabini*) tracked with geolocators from the Central Canadian Arctic (Nasaruvaalik Island) over three years (2008/09, 2010/11, 2011/12), showing mean value (range).

	Pacific Migrants	Atlantic Migrants
Migration tracks (*n*)	33	3
Departure from breeding area	18 Aug (5 Aug – 3 Sep)	24 Aug (10 Aug – 1 Sep)
Arrival at wintering area	11 Nov (15 Oct – 6 Dec)	12 Nov (10 Nov – 15 Nov)
Duration of fall migration (d)	84 (58 – 112)	84 (75 – 92)
Distance travelled (km)	14,578 (12,711 - 17,732)	14,615 (12,684 - 16,545)
Travel speed (km/day)	347 (252 – 514)	354 (345 – 362)

2.5 Discussion

Here, in the first tracking study of Sabine's gulls from the North American Arctic, I report that birds from a single colony in the central Canadian High Arctic dispersed to both the Pacific and Atlantic oceans during the non-breeding season. While the majority of tracked birds migrated west to an area of upwelling within the Humboldt Current off the coast of Peru, a small proportion of individuals migrated east to an ecologically similar area within the Benguela Current off the coasts of Namibia and South Africa. This study confirms that Atlantic-wintering Sabine's gulls breed at least as far west as the center of the Canadian Arctic (around 96° W; and vice versa for Pacific-wintering Sabine's gulls). Breeding populations with mixed migratory behaviour, such as the colony on Nasaruvaalik Island, demonstrate more diffuse migratory connectivity than would be expected for a species with such a patchy breeding distribution and disjunct wintering areas.

In the High Arctic, migratory divides occur between areas which offer an optimal combination of suitable breeding habitat balanced with a relatively low cost of migration to suitable wintering habitat, considering both the distance to travel as well as the ecological or topographical barriers en route (Gilg & Yoccoz 2010, Henningsson & Alerstam 2005, Lundberg & Alerstam 1986). This study shows that Sabine's gulls travelling from Nasaruvaalik Island to either wintering site, may incur similar energetic requirements, at least in simple terms like flying distance, speed, and duration. Throughout most of their breeding range, Sabine's gulls prefer low-lying tundra habitat associated with freshwater or tidal marshes (Day et al. 2001). Only a small portion of the

population breeds in the High Arctic (Day et al. 2001), and very little is known about Sabine's gulls breeding in the northern part of their range. A recent study by Mallory et al. (Mallory et al. 2012) however has shown that individuals breeding on Nasaruvaalik Island appear to be exploiting particularly favourable habitat, and experience higher reproductive success than birds breeding in more typical Low Arctic environments (Stenhouse et al. 2001). Nasaruvaalik Island has been identified as the most important breeding site for a wide variety of ground-nesting seabirds (including Sabine's gulls) in the Queens Channel region (Maftei et al. 2015 in press). The presence of several small but highly productive polynyas near the island provide reliable foraging opportunities even in the early part of the breeding season when surrounding waters are still completely frozen (Hannah et al. 2009, Maftei et al. 2012, Mallory et al. 2012), resulting in a small area of suitable habitat which supports a small but stable breeding population of Sabine's gulls far outside the middle of their range. Adult survival at this colony is relatively high (Fife et al. 2013) and constant across years, yet recruitment is low, indicating that this is a largely self-sustaining population. The nearest known major breeding sites lie hundreds of kilometres to the southeast and southwest (Day et al. 2001, Stenhouse et al. 2001), and the birds nesting on Nasaruvaalik Island may represent a relatively recent colonization by a diverse and distinct breeding population of birds representing the northernmost extent of both Atlantic and Pacific wintering populations.

The brief and unpredictable High Arctic breeding season places a high premium on timing arrival at the breeding site to coincide with optimal nesting conditions, and for individuals to arrive in prime breeding condition (Alerstam 2011). My study shows that in rare cases (one breeding pair tracked), mates migrate to Nasaruvaalik Island from

opposite ocean basins, with no clear indication of how the schedule of their respective partner is affected by environmental conditions en route. These mixed pairs may therefore be increasing the reproductive costs associated with failure to arrive on time and in prime condition. Even birds migrating along the same routes and relying on the same cues to time their arrival at breeding sites are susceptible to misjudging local conditions upon arrival (Morrison & Davidson 2009, Morrison 2007). Sabine's gulls form strong multi-year pair bonds (Stenhouse & Robertson 2005), and the reproductive costs involved in deferring breeding or finding a new partner if a former mate fails to arrive at the breeding site are considerable, and would presumably be exaggerated in mixed pairs arriving from different directions.

Understanding how individuals are connected between different seasons of their annual cycle (i.e. migratory connectivity; Webster et al. 2002) is essential for interpreting ecological and evolutionary patterns (Webster & Marra 2005). The strength of migratory connectivity has important conservation implications; for example events that occur at the wintering site (e.g. habitat alteration) may affect the reproductive success and survival of individuals at the breeding site (Marra et al. 2011, Rockwell et al. 2012). Information about how populations are geographically linked throughout the year is lacking for many species of migratory birds (Marra et al. 2011), including Sabine's gulls (Day et al. 2001). My research is the first to consider the degree of migratory connectivity in Sabine's gulls breeding in the Nearctic, and shows that birds breeding on Nasaruvaalik Island exhibit somewhat diffuse migratory connectivity due to mixed wintering area preference.

Ultimately, my study gives rise to a variety of ecological, behavioural and genetic questions about how the migration pathways of Sabine's gulls are determined, and on a

larger scale, how migratory behaviour of high latitude species is determined. Since migration direction tendency has only been quantified at one Canadian Arctic Sabine's gull colony (Nasuravaalik Island) and my data shows mixed migratory behaviour in adults (no juveniles have been studied), more data is needed from other colonies (east and west) and data from juvenile Sabine's gulls (particularly "hybrid" offspring) is needed in order to gain insights into the degree of inheritance and learning.

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3. Trans-equatorial Migration and Stopover Sites of Sabine's Gulls (*Xema sabini*) from the Canadian High Arctic

3.1 Abstract

Sabine's gulls (*Xema sabini*) undertake the longest migration of any gull, a spectacular trans-equatorial movement from Arctic breeding areas to pelagic wintering areas in the southern hemisphere. A recent study identified and described the routes and wintering areas used by Sabine's gulls migrating through the Atlantic, but very little is known about the population of Sabine's gulls wintering in the Pacific. My study used geolocators (n = 33) to track Sabine's gulls over three years during their annual migration from a breeding site in the Canadian High Arctic to a wintering site in the Pacific Ocean within the Humboldt Current off the coast of Peru. I quantified migration routes and timing of individual birds, identified important stopover areas used during migration, and defined the extent of their Pacific wintering area. Sabine's gulls made an average round-trip migration of over 28,000 km, travelling rapidly between highly localized stopover sites in areas of coastal upwelling. The Juan de Fuca Eddy off the southwest coast of British Columbia was identified as the most important stopover site, used by birds during both spring and fall migration. All of the Pacific migrants tracked spent the winter within a relatively restricted area of upwelling within the Humboldt Current off the coast of Peru. Tracks also confirmed that some Sabine's gulls make a remarkable overland (3268 km) spring migration crossing multiple mountain ranges between the Pacific Ocean and Hudson Bay or the Bering Sea en route to the breeding site in the Canadian High Arctic.

3.2 Introduction

Understanding a species' migration pattern, such as timing of movements and the routes and stopover areas used, may help to predict or explain changes in population size or distribution. Seabirds, many of which are long-distant migrants, continuously target areas of high marine productivity throughout their annual cycle (González-Solís et al. 2007, McKnight et al. 2013, Shaffer et al. 2006), and therefore aggregate where resources are available and predictable, e.g. areas of strong coastal upwelling and steep continental slopes or shelf breaks (Burger 2003, Duffy 1989, Vermeer et al. 1989).

Unique among Larids, Sabine's gulls (*Xema sabini*) undertake a lengthy trans-equatorial migration between Arctic breeding sites and pelagic wintering areas in the southern hemisphere - the longest migration of any gull (Stenhouse et al. 2012). Although Sabine's gulls breed at mostly small scattered colonies across a wide circumpolar range (Day et al. 2001), they are only known to winter in two distinct areas in the Southern hemisphere; within the Humboldt Current off the coast of Peru in the Pacific (Chapman 1969, Day et al. 2001), and within the Benguela Current off the coast of South Africa in the Atlantic (Lambert 1972, Stenhouse et al. 2012). Recently, geolocators were used to track the migration of Sabine's gulls breeding in Eastern Greenland to the Atlantic wintering site, revealing the timing and routes of their migration, the extent of their wintering range, and stopover areas used during fall and spring migration (Stenhouse et al. 2012). In Chapter 2, I showed for the first time where birds breeding at a site in the Central Canadian Arctic spend the non-breeding season. Detailed information on the movements of Sabine's gulls wintering in the Pacific continues to be deficient,

specifically the routes and timing of their migration as well as distance and speed travelled.

In this study I used geolocators to track the migration of Sabine's gulls from a breeding colony in the central Canadian Arctic to their Pacific wintering site. Specifically, my objectives were (1) to identify the route(s) used by Sabine's gulls from a Canadian Arctic breeding site to and from their wintering area in the Pacific, (2) to quantify the timing of these migrations, the distance and speed travelled during the nonbreeding period, as well as the sex-related variation in migration timing, (3) to identify the stopover areas used during fall and spring migration, and define the extent of their wintering area.

3.3 Methods

Study site

I captured Sabine's gulls on Nasaruvaalik Island, Nunavut, (75.8˚ N, 96.3˚ W), between early June and late August over five years (2008-2012). The study site is described in Chapter 2 (see Figure 2-1) and in detail in Mallory et al. (2012).

Deployment and recovery of geolocators

As previously described in Chapter 2, I deployed 47 geolocators (44 LAT2900 and 3 LAT2500, Lotek Wireless, Canada) on 36 adult breeding Sabine gulls on Nasaruvallik Island over three years (two in 2008, 23 in 2010, and 21 in 2011). In total, I deployed geolocators on 18 females and 18 males, 11 of which (six males and five females) I

tagged twice. I captured breeding Sabine's gulls with a spring-loaded bow net (Bub 1991) or a handheld CO_2 powered net gun (see Edwards & Gilchrist 2011 for details). I captured breeding Sabine's gulls with a spring-loaded bow net (Bub 1991) or a handheld CO_2 powered net gun (see Edwards & Gilchrist 2011 for details). I attached geolocators to Darvic tarsal bands with plastic cable ties, totaling 2.1g (LAT2900) and 3.8g (LAT2500), averaging 1.1% and 2.0% of adult body weight respectively. All tagged birds were also fitted with a numbered metal band and a unique combination of Darvic bands on the opposite leg. I weighed birds using a 300-g Pesola spring scale and measured culmen, total head length, wing chord, and tarsus (mm). I determined the sex of tagged birds through an analysis of 2-3 drops of blood collected from the brachial vein (as described by Quintana et al. 2008). I recaptured tagged birds the following year to recover the geolocators (one unit was recovered after two years), and downloaded the data in LAT Viewer Studio© (Lotek Wireless, Canada).

Tag Effect

I assessed the effect of geolocators on Sabine's gulls by comparing return rate and date, adult body mass change, nest success, and chick growth between tagged and control birds. I weighed Sabine's gulls at tag deployment and recovery, made daily checks for individually colour-marked birds present within the study area, marked and monitored nests to determine nest success (see Mallory et al. 2012 for detailed methods), and banded and weighed recently hatched chicks to calculate chick growth. I defined treatment nests

as nests with either one or two tagged parents, and control nests as nests without tagged parents (see Appendix 1 for detailed *Tag Effect* methods).

Data processing

The geolocators used in this study estimated location once daily; latitude was estimated from the duration of daylight between sunset and sunrise, and longitude from the exact time of sunrise and sunset (Ekstrom 2004). The geolocators sampled sea-surface temperature (SST) when immersed for more than two consecutive samples (i.e. 120 s) and recorded the minimum daily value (°C) (Lotek Wireless 2010). As described in Chapter 2, I used SST correlation (LAT Viewer Studio©) to improve the accuracy of latitude estimates based on the approach used by Shaffer et al. (2005), which allowed me to retain data around the equinoxes. I used 8-day composites of nighttime SST grids from the MODIS TERRA satellite in this study (http://whiteshark.stanford.edu/public/lotek_sst/, 4 km resolution), which are suitable for comparison to the tag values (Warnock 2010). I then filtered locations (Freitas 2012) to remove positions implying an unrealistic flight speed in Program R (R Core Team 2013). I assumed Sabine's gulls did not exceed a maximum velocity of 13.9 m/s (> 50 km/h sustained over a 48 h period) (Hedenström 1998). To further reduce the mean error in positions estimates, I smoothed each track using a moving weighted average (with a window size of three), whereby each smoothed position was the weighted average (in a 1:2:1 ratio) of the previous, current, and subsequent position (as per Fifield et al. 2014). Fixed start positions (at breeding colony) and positions that showed large daily

movements (greater than 4° of longitude or 6° degrees of latitude) were not smoothed to avoid introducing positional errors (Phillips et al. 2004).

Analysis of movement data

As described in Chapter 2, I pooled all valid locations and generated kernel density estimations to represent the annual distribution of tracked birds (ESRI ArcGIS 10.1, search radius: 200 km, output cell size: 10 km). I created occupancy contours (25, 50, 75%) in Geospatial Modelling Environment (GME; Beyer 2012) to determine areas of high use throughout the annual cycle. I used the 50% occupancy contour generated around the known Pacific wintering area in the Southern Hemisphere (Day et al. 2001) to set the boundary for the "wintering area". Tracked Sabine's gulls that migrated to the Atlantic for the winter were not included in the remaining analysis (see Chapter 2 for full discussion of Atlantic migrating Sabine' gulls).

Using previously assigned location categories ("stopover" or "travel", see Chapter 2), tracks were split into three periods; fall migration, winter, and spring migration. Fall migration was defined as the period between departure from the breeding area (i.e., first "travel" location identified after breeding period) and arrival to the wintering area (i.e., first "stopover" location within the pre-defined wintering area). Spring was similarly defined as the period between departure from the wintering area and arrival to the breeding area (as per Fifield:2014bj and Ramírez et al. 2013). All stopover periods were further categorized as "primary" if more than 75% of tracked birds used a particular area. For each primary fall and spring stopover area, I generated kernel density estimations

(ESRI ArcGIS 10.1) using a search radius of 200 km and an output cell size of 10 km, which is comparable to similar studies (Gilg et al. 2013, Hedd et al. 2012, Stenhouse et al. 2012). To represent the distribution of birds at primary stopover areas, I created 25%, 50%, and 75% occupancy contours (GME; Beyer 2012). The Pacific wintering site occupancy contours were previously generated in Chapter 2.

In addition to travel distance (km) and travel speed (km/d) calculations done in Chapter 2 (calculations that do not include movement during stopover periods), I calculated migration distance (km) and migration speed (km/d). Migration distance was defined as the total distance travelled during fall or spring migration, including stopover movement and migration speed (km/d) as the migration distance divided by the number of days (including "stopover" days) migrated during fall or spring migration (as per Fijn et al. 2013). All distance (great-circle) calculations were done in Program R (R Core Team 2013).

3.4 Results

Geolocator recovery and data details

As previously reported in Chapter 2, I recovered 38 of 47 (81%) geolocators deployed on Nasaruvaalik Island (Table 3-1). Four additional birds were seen at the breeding site with a geolocator but I was unable to capture them (non-breeding) and one bird showed up to breed but had lost the geolocator (92% of tags were re-sighted). Two of the birds tracked (three tracks) did not winter in the Pacific (see Chapter 2 for the results of Atlantic birds).

Table 3-1. Details of Sabine's gulls (*Xema sabini*) tracked with geolocators (*n* = 33) from Nasaruvaalik Island in the Canadian High Arctic.

Year	Band	Sex	First Valid Fix	Last Valid Fix	Unfiltered Locations	Filtered Locations	Valid Locations (%)
2008/ 2009	69921[a]	M	01-Sep	15-Jun	288	282	97.9
	69923	M	03-Sep	08-Jun	279	261	93.5
	69926	M	30-Aug	07-Jun	282	275	97.5
2010/ 2011	69953[b]	F	23-Aug	12-Dec	112	102	91.1
	69902[c]	F	11-Aug	31-Jan	174	160	92.0
	69905[d]	F	21-Aug	09-Jun	293	250	85.3
	69909	F	14-Aug	03-Mar	202	187	92.6
	69913[e]	M	09-Aug	26-Jan	171	142	83.0
	69914	F	10-Aug	14-Nov	97	85	87.6
	69915[f]	F	07-Aug	08-Mar	214	190	88.8
	69919[g]	M	26-Aug	08-Nov	75	58	77.3
	69920	M	09-Aug	12-Oct	65	60	92.3
	69921[a]	M	21-Aug	25-Feb	189	175	92.6
	69924	M	11-Aug	15-May	278	255	91.7
	69925	F	15-Aug	15-Oct	62	58	93.5
	69985	F	07-Aug	29-Jan	176	165	93.8
	69991	F	07-Aug	16-Oct	71	61	85.9
	69992	M	19-Aug	08-Jan	143	137	95.8
	69993	M	11-Aug	05-Apr	238	226	95.0
	69994[h]	M	11-Aug	17-Jun	311	250	80.4
2011/ 2012	69953[b]	F	21-Aug	13-Jun	298	265	88.9
	69902[c]	F	18-Aug	09-Apr	236	222	94.1
	69905[d]	F	13-Aug	22-Oct	71	64	90.1
	69913[e]	M	31-Aug	15-Jun	290	271	93.4
	69915[f]	F	13-Aug	04-Oct	53	49	92.5
	69919[g]	M	31-Aug	15-Jun	290	267	92.1
	69923	M	02-Sep	26-Jan	147	129	87.8
	69928	F	22-Aug	08-Jun	292	273	93.5
	69979	F	19-Aug	22-Jun	309	286	92.6
	69994[h]	M	25-Aug	06-Apr	226	219	96.9
	71302	M	31-Aug	12-Jun	287	273	95.1
	71303	F	21-Aug	08-Jun	293	277	94.5
	71307	F	23-Aug	19-Sep	28	28	100.0
	Mean		18-Aug	3-Mar	198	182	91.5
	Total		-	-	6,540	6,002	91.8

[a-h] birds tagged for a second year

After filtering, my dataset contained 6,002 locations (91.8% valid), averaging 182 days per track (Table 3-1). Eleven of the recovered geolocators gave a full year of migration data, two provided partial spring migration, 15 provided fall migration and wintering data only, eight provided partial fall migration, and two failed during the breeding season and were not included in the analysis (n = 33; Table 3-1). Eight birds were tracked twice; therefore my data describes the movement of 25 individual birds.

Tag effect

There was no significant difference in return rate and return date between tagged and untagged birds, or in nest success and chick growth between treatment and control nests (see Appendix 1 for details). When the 2.1 g LAT2900 tags were used (n = 44), there was no difference in the mean body weight of tagged birds between tag deployment and recovery, however when the 3.8 g LAT2500 tags were used (n = 3), there was a significant decrease in body weight of tagged birds (-10.3 g change, $t_2 = 7.75$, p = 0.02).

Migration pattern

In general, Sabine's gulls followed a coastal migration route from the breeding site in the Canadian High Arctic to the wintering site off the coast of Peru (Figure 3-1). Throughout their annual migration, Sabine's gulls demonstrated a stepping-stone pattern of migration, where travel periods (Figure 3-1; blue) were frequently interrupted by stopover periods (Figure 3-1; red).

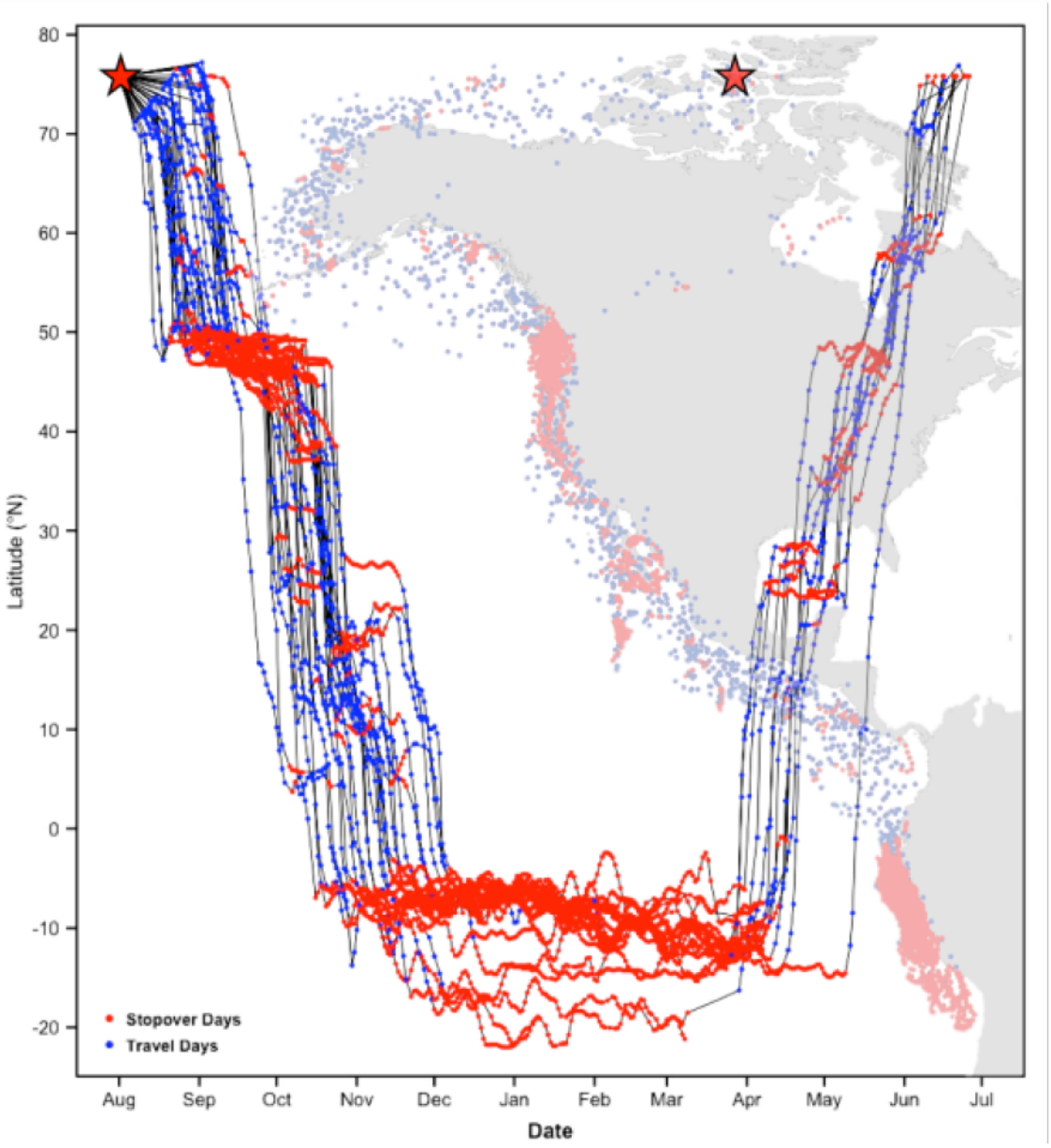

Figure 3-1. Annual migration of Sabine's gulls tracked with geolocators (n = 33), from a breeding site in the Canadian High Arctic (red star) to the Pacific wintering site off the coast of Peru, showing travel days (blue) frequently interrupted by stopover days (red), showing individual variation in timing and latitude of migration. Faded map in background shown for geographic reference only.

Fall (southbound) migration and stopover

Tagged Sabine's gulls began post-breeding migration in mid-August (Table 3-2). Birds headed west from the breeding area, following the coast of Alaska south to the Pacific Ocean (Figure 3-2). By early September (Table 3-2), all birds had arrived at the primary fall stopover site within the Juan de Fuca Eddy off the southwest coast of Vancouver Island (Figure 3-2 inset). This area was used by 100% (n = 33) of the tagged birds during southbound migration, and individuals stopped for an average of 31 days (± 11.4 d; Table 3-2). The 50% fall stopover occupancy contour (core use) represented an area of 94,101 km^2, ranging from 50.0 ˚N to 45.6 ˚N (mean 47.8 ± 1.2 ˚N) and 126.7 ˚W to 123.8 ˚W (mean 125.2 ± 0.6 ˚W) (Figure 3-2 inset). In early October (Table 3-2), birds continued their migration south along the Pacific coast of North and Central America, before crossing the equator to arrive at the wintering area off the coast of Peru (Figure 3-3), in mid-November (Table 3-2). Southbound migration (n = 26) was completed in an average of 84 days (± 15.2 d; Table 3-2).

Wintering Area

Sabine's gulls spent almost five months (mean 146 ± 15 d) wintering off the coast of Peru, beginning in mid-November and ending in early April (Table 3-2). The 50% winter area occupancy contour (core use) represented an area of 167,637 km^2, ranging from 5.2 ˚S to 11.4 ˚S (mean 7.9 ± 1.5 ˚S) and 82.7 ˚W to 79.1 ˚W (mean 80.8 ± 0.8 ˚W) (Figure 3-3).

Table 3-2. Migration details of Sabine's gulls (*Xema sabini*) tracked with geolocators from a breeding site in the Canadian High Arctic (Nasaruvaalik Island) over three years (2008/09, 2010/11, 2011/12).

		Mean	Range	SD	*n*
Fall	Start fall migration	18 Aug	5 Aug – 3 Sep	8.7	33
	Arrive Juan de Fuca	6 Sep	19 Aug – 29 Sep	11.4	33
	Depart Juan de Fuca	5 Oct	12 Sep – 24 Oct	9.4	32
	Duration of fall stopover (d)	31	6 – 54	11.4	32
	End fall migration	10 Nov	14 Oct – 5 Dec	15.5	26
	Duration of fall migration (d)	84	58 – 112	15.2	26
	Distance of fall travel (km)	14,578	12,711 – 17,732	1,092	26
	Speed of fall travel (km/day)	347	252 – 514	63	26
Winter	Arrive Humboldt	11 Nov	15 Oct – 6 Dec	15.5	26
	Depart Humboldt	8 Apr	24 Mar – 9 May	11.5	13
	Duration of winter (d)	146	123 – 178	14.8	13
Spring	Start spring migration	9 Apr	25 Mar – 10 May	11.5	13
	Arrive Juan de Fuca	14 May	28 Apr – 21 May	6.8	12
	Depart Juan de Fuca	22 May	16 May – 29 May	4.4	11
	Duration of spring stopover (d)	9	5 – 19	3.6	11
	End spring migration	18 Jun	9 Jun – 25 Jun	5.0	13
	Duration of spring migration (d)	74	55 - 92	11.8	13
	Distance of spring travel (km)	13,800	11,694 – 16,671	1,309	11
	Speed of spring travel (km/day)	318	266 - 362	33	11
Annual	Annual travel (excl. stops, km)	28,330	25,807 – 31,968	1,706	11
	Annual migration (incl. stops, km)	37,393	34,831 – 41,407	1,843	11

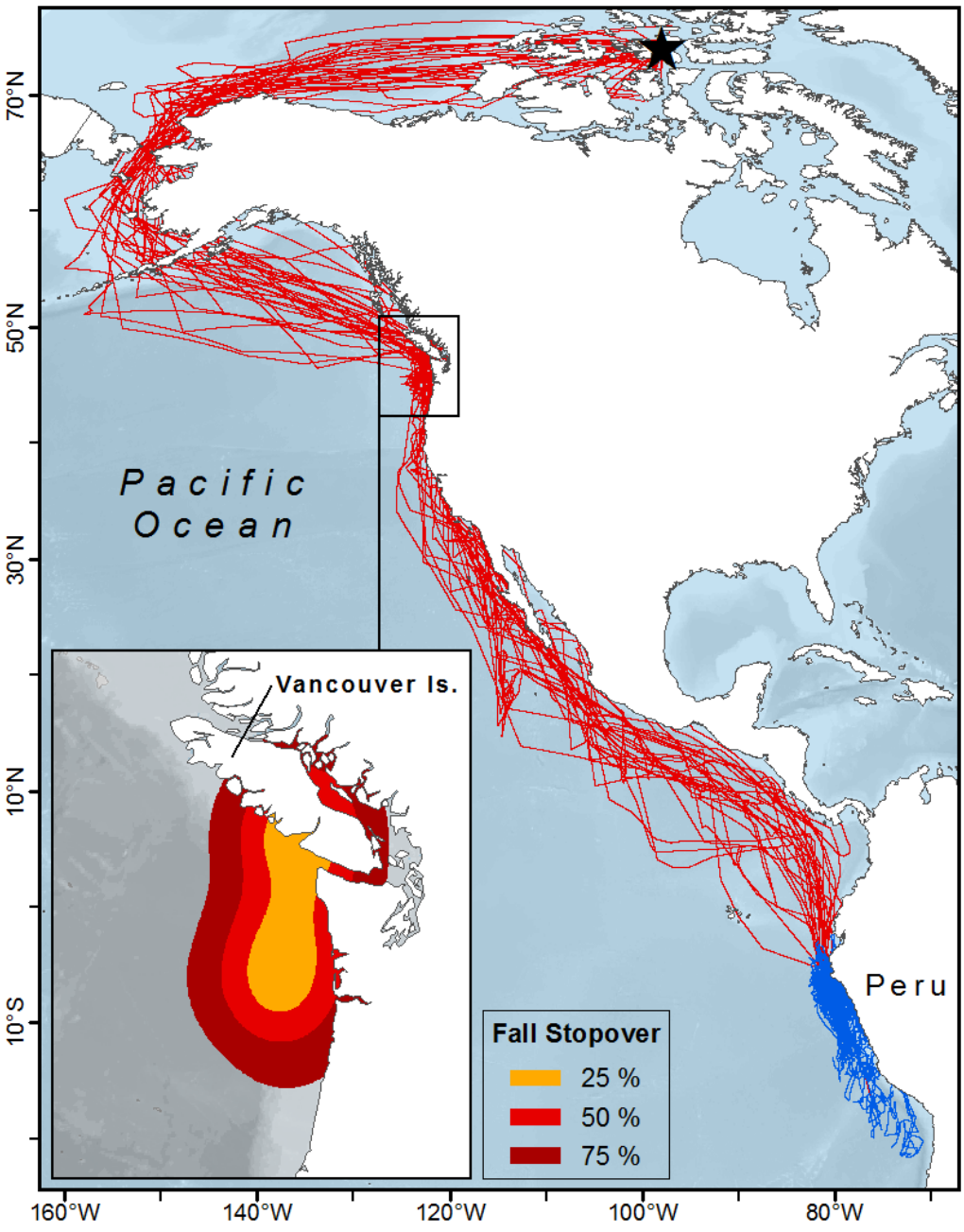

Figure 3-2. Southbound migration of Sabine's gulls from Nasaruvaalik Island, Nunavut, to the Pacific wintering area off the coast of Peru over three years (2008/09, 2010/11, 2011/12). Fall migration (red, *n* = 33), winter movement (blue, *n* = 26). Inset map shows the primary fall stopover area, with 25%, 50%, and 75% occupancy contours (Winkel-Tripel projection).

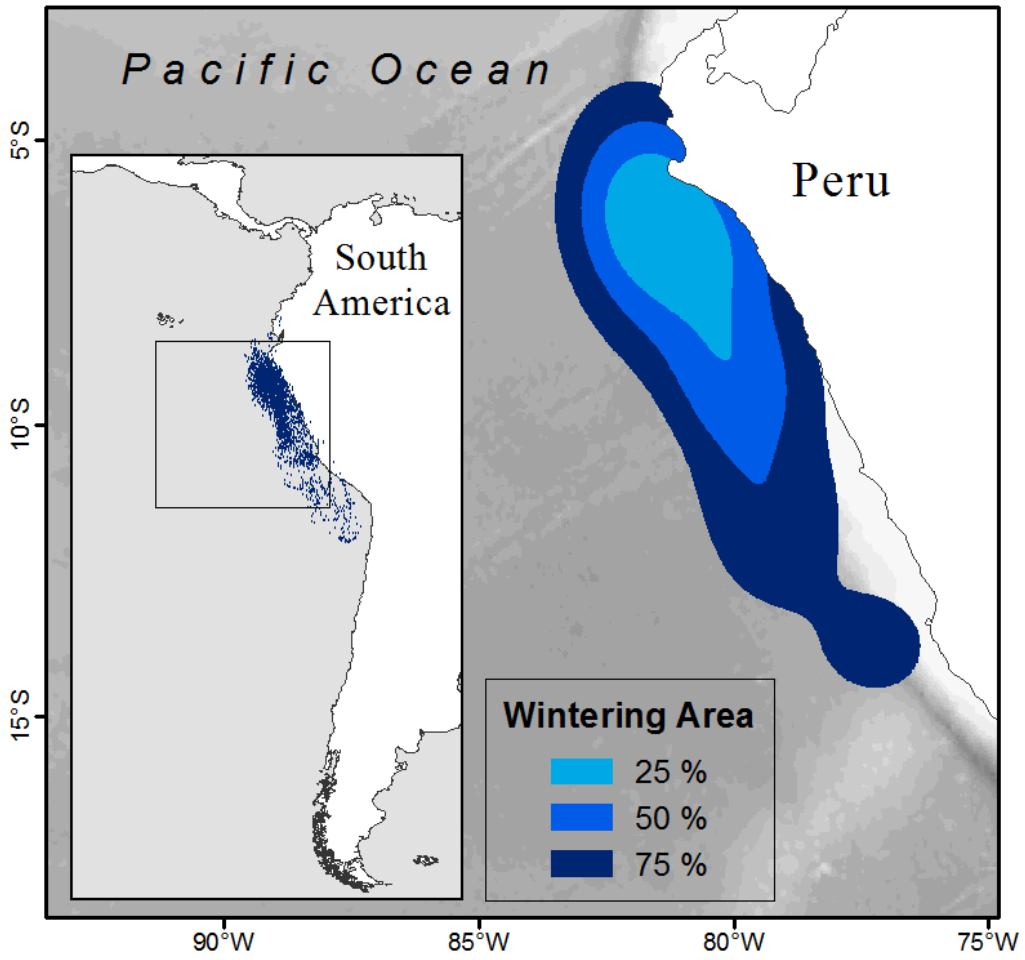

Figure 3-3. Wintering area of Sabine's gulls (*n* = 26) from a breeding site in the Canadian High Arctic over three years (2008/09, 2010/11, 2011/12), showing the 25%, 50%, and 75% winter occupancy contours (main) and all winter locations (inset) (South America Albers Equal Area projection).

Spring (northbound) migration and stopover

Northbound migration began in early April (Table 3-2), with birds following a route along the west coast of Central and North America (*n* = 13; Figure 3-4). Individuals stopped again within the Juan de Fuca Eddy off the southwest coast of Vancouver Island in mid-May, remaining at this primary spring stopover area for 9 days (± 3.6 d; Table 3-2, Figure 3-4 inset). This stopover area was used by 12 of the 13 birds tracked (92%) during northbound migration. The 50% spring stopover occupancy contour (core use) represented an area of 222,806 km^2, ranging from 49.0 ˚N to 45.5 ˚N (mean 47.5 ± 0.9 ˚N) and 128.3 ˚W to 124.0 ˚W (mean 126.0 ± 1.0 ˚W; Figure 3-4 inset). Birds departed the stopover area at the end of May, and were observed arriving back on Nasaruvaalik Island in mid-June (Table 3-2). Northbound migration (*n* = 13) was completed in an average of 74 days (± 11.8 d; Table 3-2).

Overland Migration

In the final leg of the northbound migration, tagged Sabine's gulls followed three extremely different routes (Figure 3-4). Two birds roughly retraced their southbound tracks around the coast of Alaska, but eight other birds (in two different years), incorporated significant overland flights on their way back north. Most remarkably, two birds flew directly east overland from the spring stopover area off the coast of Vancouver Island (late May) to Hudson Bay (early June), travelling an average distance of 3268 km (3142 to 3394 km; Figure 3-4). On this route, one of the birds stopped for 4 days (31 May to 3 Jun) in northern Saskatchewan, while the other flew non-stop for 10 days (mean

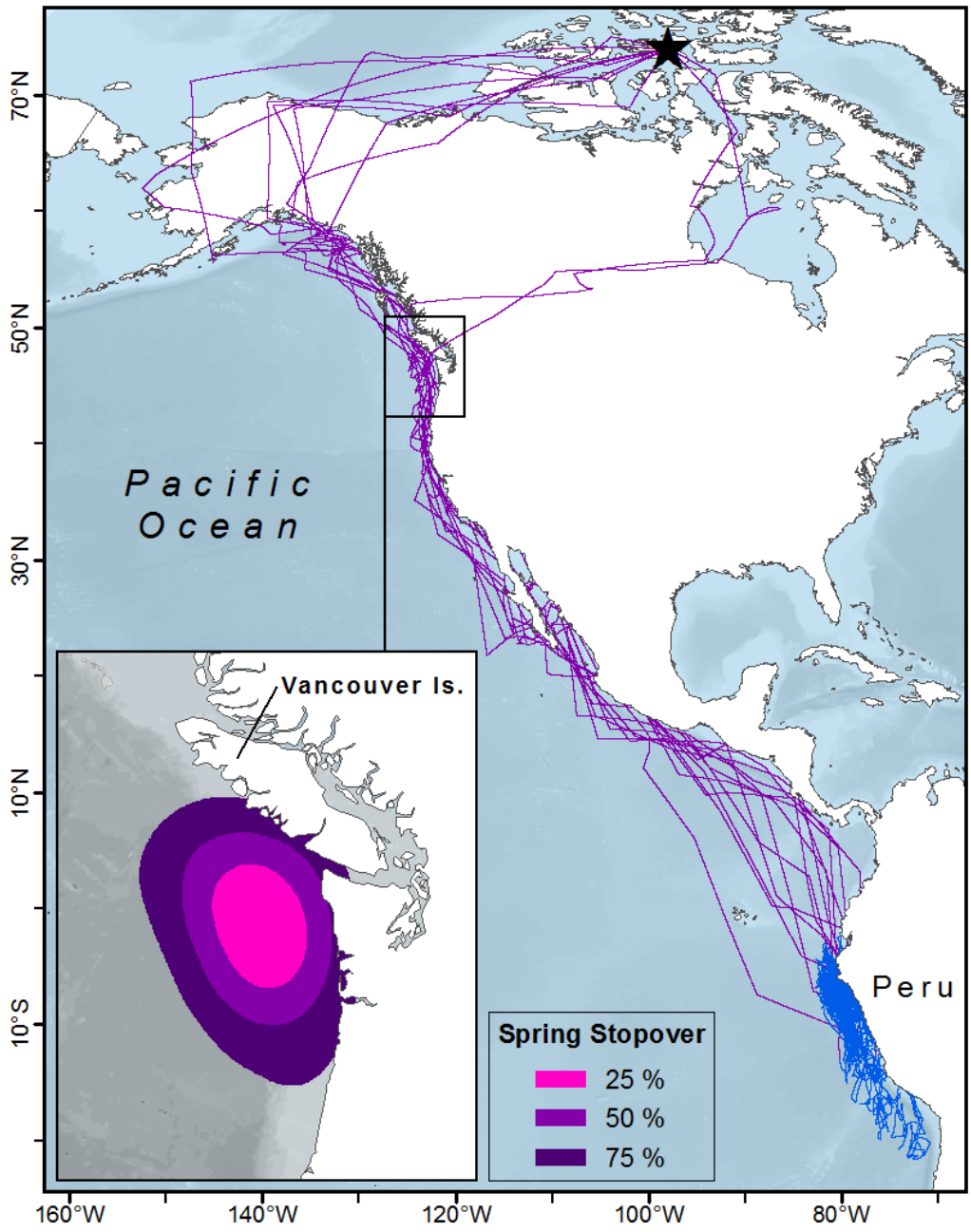

Figure 3-4. Northbound migration of Sabine's gulls from the Pacific wintering area off the coast of Peru to Nasaruvaalik Island, Nunavut over three years (2008/09, 2010/11, 2011/12). Spring migration (purple, *n* = 33), winter movement (blue, *n* = 26). Inset map shows the primary spring stopover area, with 25%, 50%, and 75% occupancy contours (Winkel-Tripel projection).

travel speed 311 km/d; 286 to 339 km/d). Upon arrival to Hudson Bay, both birds stopped for 6-8 days before flying almost due north to the breeding site on Nasaruvaalik Island (Figure 3-4).

The other six birds appeared to rapidly cross interior Alaska between the Gulf of Alaska and the Beaufort Sea (Figure 3-4). At this latitude (> 60 °N) on dates approaching the summer solstice (24 h daylight), geolocation estimates tend to be inaccurate, but corresponding SST data showed an abrupt temperature change from 5.6 ± 1.7 °C on the last valid date within the Gulf of Alaska (3 Jun ± 3.1 d) to -0.8 ± 1.0 °C on the first valid date within the Beaufort Sea (6 Jun ± 3.0 d). The rapid movement of these Sabine's gulls from warmer waters to sub-zero waters (in 3 d ± 1.4 d) can only be explained by an overland route, since a coastal route around Alaska through the eastern Aleutian Islands North to the Beaufort Sea greatly exceeds the maximum known flight speed for Sabine's gulls.

Variation in migration timing

In 2010, severe weather conditions during the early chick-rearing period caused widespread chick mortality and ultimately total colony failure. The entire breeding colony was subsequently abandoned by early August. By comparison, birds were still actively rearing chicks throughout August of 2008 and 2011. Birds tagged in the failed year (2010) departed the breeding area 10 days earlier than birds tagged in successful years (2008 and 2011) (14 Aug ± 7 d vs. 24 Aug ± 7 d, $t_{31} = -4.1$, $p < 0.001$).

I also tested for differences in migration timing between the sexes in 2010/11 and 2011/12 tagged birds (2008/09 tagged birds were all male). Females departed the breeding area earlier than males in 2011 (17 Aug ± 4 d vs. 29 Aug ± 3 d, $t_{10} = -6.1$, $p < 0.001$), but not in 2010 when the entire colony failed. Females arrived at the wintering area earlier than males in both years (4 Nov ± 16 d vs. 17 Nov ± 13 d, $t_{21} = -2.3$, $p < 0.05$). Most geolocators failed before recording a full year of data, but observations of colour marked birds returning to the breeding site for 2011 and 2012 (17 females, 16 females) indicated that males arrived back on Nasaruvaalik Island five days earlier than females (18 Jun ± 4 d vs. 23 Jun ± 5 d, $t_{30} = 3.2$, $p < 0.01$).

Migration distance and speed

During fall migration, birds travelled an average of 14,578 km at a speed of 347 km/day, and during spring migration, birds travelled an average of 13,800 km at a speed of 318 km/day (excluding stopover movement) (see Table 3-2 for s.d. and range, Figure 3-5, Figure 3-6). While birds were within stopover areas (fall, winter, spring), movement speed averaged 45 ± 6 km/day (range 28 to 73 km/d; Figure 3-6). Over their entire annual migration, tagged Sabine's gull flew 28,330 km excluding stopover movement, and 31,363 km when stopover movement was included (see Table 3-2 for s.d. and range). There was no statistically significant difference between the migration distance or migration speed between sexes (all p-values > 0.05).

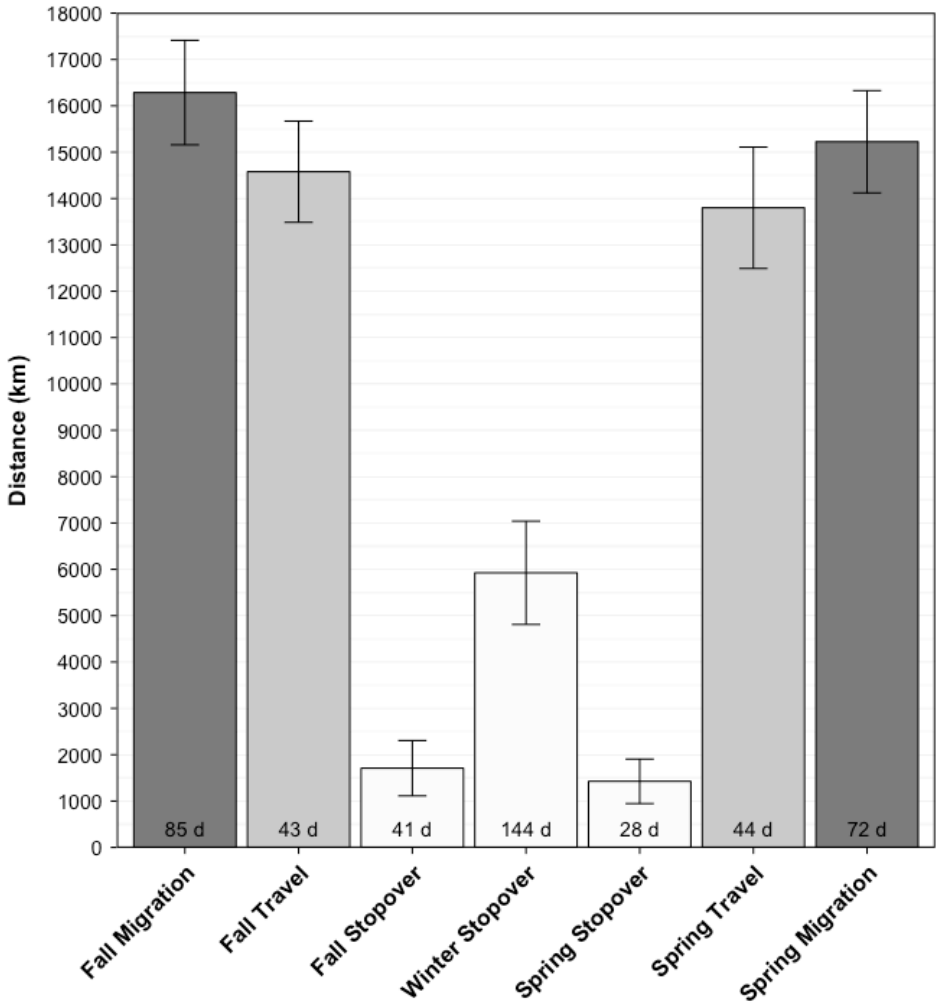

Figure 3-5. Mean distances (km) and duration (days) flown by Sabine's gulls during migration in 2008 - 2012 from a breeding site in the Canadian Arctic to their wintering site off the coast of Peru (fall *n* = 26, winter *n* = 13, spring *n* = 11). "Migration" distance was defined as the total distance travelled during each stage (including stopover movement), while "travel" distance was defined as the distance travelled between stopover periods (excluding stopover movement).

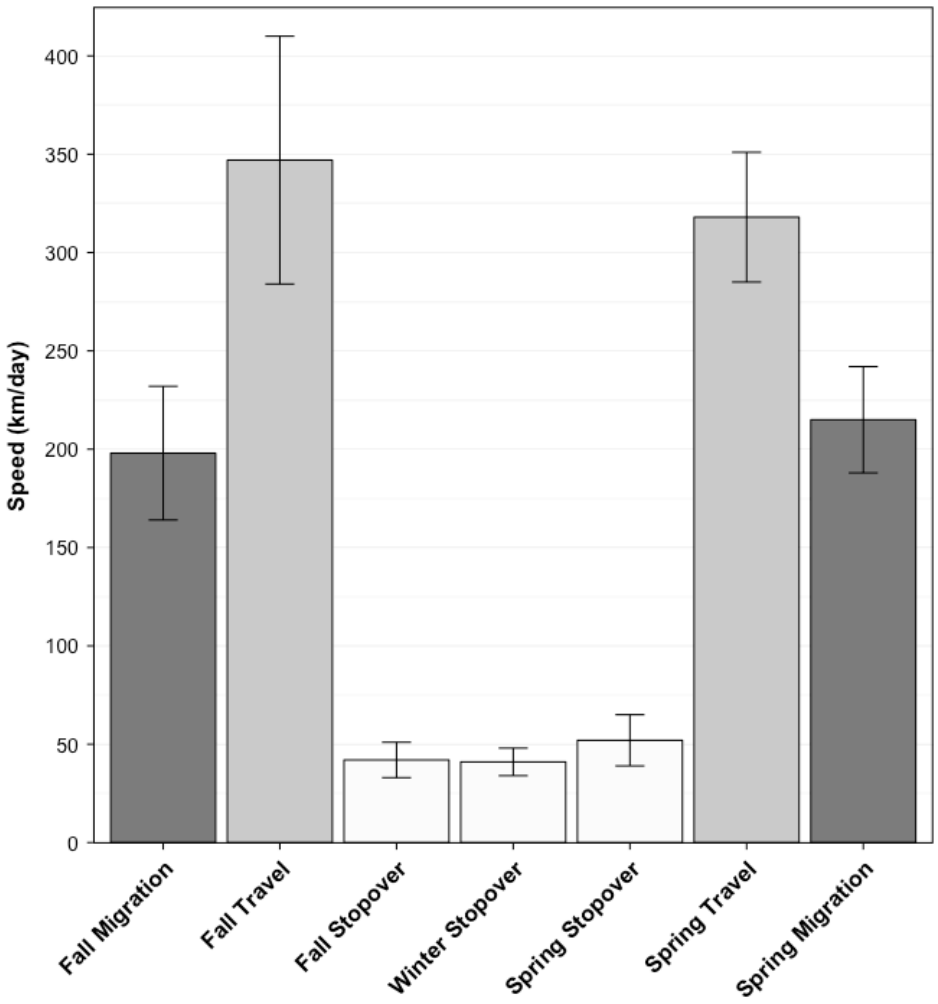

Figure 3-6. Mean speed (km/day) of Sabine's gulls during migration in 2008 - 2012 from a breeding site in the Canadian Arctic to their wintering site off the coast of Peru (fall *n* = 26, winter *n* = 13, spring *n* = 11). "Migration" speed was defined as the migration distance divided by the number of migration days, including stopovers, while "travel" speed was defined as the travel distance divided by the days travelled between stopover periods.

3.5 Discussion

My study tracking the Pacific migration of Sabine's gulls from a breeding site in the Canadian High Arctic indicated that these birds followed a coastal, trans-equatorial migration to an area off the coast of Peru, travelling more than 28,000 km annually. Birds move rapidly between stopover sites characterized by highly productive upwelling areas within the Eastern Pacific ocean and most importantly, use the Juan de Fuca Eddy as their primary fall and spring stopover site. I have also confirmed for the first time that Sabine's gulls are capable of long-distance overland movements.

Trans-equatorial migration

While trans-equatorial migration is a fairly common strategy employed by many families of birds that travel between areas of alternating high seasonal productivity (Gilg et al. 2013, Hedd et al. 2012, Mellone et al. 2013), it is a relatively rare among the Laridae, which are mostly short-distance migrants (Hatch et al. 2011, Klaassen et al. 2011), and as a group tend to be highly adaptable and opportunistic scavengers (Karnovsky et al. 2009, Villablanca et al. 2007). Only Sabine's gulls and Franklin's gulls (*Larus pipixcan*) are known to undertake long, trans-equatorial migrations, the latter of which breeds in the prairie regions of North America and migrates south to coastal regions of Peru (Burger 2010, Howell & Dunn 2007). There are, however, several notable exceptions within the closely related Sternidae and Stercoraridae, including the Arctic tern (*Sterna paradisaea*) which completes the longest known annual migration of any bird (Egevang et al. 2010, Fijn et al. 2013), while Pomarine, Parasitic, and Long-tailed jaegers (*Stercorarius pomarinus, S. parasiticus, S. longicaudus*) also breed in the northern hemisphere and

winter in the southern hemisphere (Gilg et al. 2013, Olsen & Larsson 1997). The related south polar skua (*Stercorarius maccormicki*) breeds in the southern hemisphere and winters in the northern hemisphere (Kopp et al. 2011). It is notable that all of these species are highly pelagic during the non-breeding season, and it is likely that the risks and demands of a lengthy annual migration are offset by the benefits of targeting areas of extremely high seasonal productivity in which there is little direct competition for resources.

Wintering and stopover habitat

My results are consistent with previous research by Stenhouse et al. (2012) and confirm that Sabine's gulls target areas of strong and predictable upwelling during their migrations, and are restricted to localized areas of similar habitat during the winter. While many seabirds show a clear affinity for productive areas of upwelling (Kopp et al. 2011, Shaffer et al. 2006), Sabine's gulls are less adapted to a truly pelagic lifestyle than alcids that can dive deep below the surface to expand their vertical foraging range (Croll et al. 1992) or tubenoses that can travel efficiently across wide expanses of unproductive waters while scavenging opportunistically in areas of unpredictable or ephemeral food abundance (Dias et al. 2012, Phillips et al. 2008). As such, Sabine's gulls may be particularly dependent on areas in which strong upwelling concentrates large zooplankton and small fish close to the surface for the duration of the non-breeding season. The reliance of Sabine's gulls on areas of high marine productivity has already been shown in the Atlantic population of the species. These birds winter within the Benguela Current off the coast of South Africa and stage in the Bay of Biscay off the coast of Portugal in the

fall, and within the Canary Current off the coast of Northwest Africa in the spring (Stenhouse et al. 2012). The Pacific wintering area I identified for Sabine's gulls within the Humboldt Current off the coast of Peru is similarly an area of high primary productivity supporting high forage fish populations (Daneri et al. 2000), and offers surface foraging seabirds like Sabine's gulls predictable access to abundant resources (Weichler 2004)

The primary stopover site used by tracked Sabine's gulls over the continental shelf off southwest Vancouver Island during both spring and fall migration is another area characterized by strong coastal upwelling conditions and known for its extremely high productivity (Burger 2003, MacFadyen et al. 2008). The unique currents and bathymetry in the Juan de Fuca region creates a large cyclonic eddy (the Juan de Fuca Eddy) which forms in the spring and persists until the fall (MacFadyen et al. 2008, Pool et al. 2008), and is responsible for massive upwelling of deep, nutrient-rich water rising up from the Juan de Fuca Canyon (Freeland 1992, Pool et al. 2008). The cold, upwelled water spreads over an extensive and shallow bank at the edge of the continental shelf (Swiftsure Bank), creating exceptionally favourable conditions for foraging seabirds, whales, and fish (Burger 2003, Vermeer et al. 1989).

Overland Migration

Although Sabine's gulls are highly pelagic away from their breeding areas (Day et al. 2001), a surprising result of my study was the discovery that at least some individuals follow an overland migration route across Canada between the coast of British Columbia and Hudson Bay or across Alaska between the Gulf of Alaska and the Bering Sea. This

strategy involves crossing the considerable obstacles presented by the Coastal and Rocky mountain ranges and the Brooks Range, respectively. Similar overland 'shortcut' routes have also recently been documented in Arctic terns which cross over the Andes mountains from west to east instead of rounding Cape Horn en route between stopover sites in the Pacific and wintering areas in the Southern Ocean (Duffy & McKnight 2013). While such overland movements are not without precedent in otherwise pelagic seabirds (Duffy & McKnight 2013), it demonstrates a unique plasticity in Sabine's gulls which appear to be able to make on route decisions to following alternate coastal or overland migration routes as ice and weather conditions dictate on a year-to-year basis. An overland route may allow birds to reach High Arctic breeding sites faster in the spring, as well as maximizing the likelihood of encountering favourable foraging opportunities in freshwater lakes or early thawing inlets around river mouths in Hudson Bay at a time when large sections of the ocean at northern latitudes remain frozen and inhospitable.

The rare but regular presence of Sabine's gulls in late May and early June in areas of northern inland Canada, far from known breeding areas, has been previously noted (Day et al. 2001, Savile 1972, Taylor 1972, Wolford 1972), but never conclusively explained. My confirmation of an overland flight path used by Sabine's gulls travelling between the Pacific and Hudson Bay firmly put these reports into context.

Conservation implications

Although Sabine's gulls are not currently threatened in Canada, they are highly dependent on a few localized areas of high marine productivity throughout their annual cycle. Understanding the details of Sabine's gull migration informs conservation efforts

by identifying important habitats, as well as overlapping human activities and potential environmental and anthropogenic threats. The Juan de Fuca Eddy and the northern Humboldt current region must in this context be recognized as particularly important sites for Sabine's gulls and the main area of conservation concern outside the breeding season. These areas also host large numbers of other seabirds, including other long-distance migrants such sooty shearwaters (*Puffinus griseus*) (Shaffer et al. 2006) and Arctic terns (McKnight et al. 2013), highlighting the importance of productive upwelling sites in the Pacific Ocean.

3.6 Literature cited

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4. Summary and General Discussion

4.1 Thesis Summary

Sabine's gulls undertake the longest migration of any gull, a spectacular trans-equatorial movement from Arctic breeding areas to pelagic wintering areas in the southern hemisphere. All breeding populations are known to winter in either of two geographically disparate but ecologically similar areas: the Humboldt Current off the coast of Peru, and the Benguela Current off the coast of South Africa. Despite considerable speculation, it has never been confirmed where the migratory divide for this species lies in the Nearctic (or even if there is a disctinct migratory divide as opposed to a wide area of mixed migration tendency), and to what extent gaps in the non-contiguous circumpolar breeding range may reflect segregation of wintering populations. A recent study (Stenhouse et al. 2012) identified and described the routes and wintering areas used by Sabine's gulls (n = 10) migrating through the Atlantic, but very little is known about the breeding population of Sabine's gulls in the Canadian High Arctic, and birds migrating through the Pacific have never before been studied in detail.

The goal of my thesis was to examine the movement and distribution of Sabine’s gulls from the Canadian High Arctic. This research answered three important questions regarding Sabine’s gull movement during the non-breeding season, specifically filling gaps in our knowledge about this species, as well as increasing our understanding of the migratory connectivity of circumpolar species and ecology of pelagic seabirds.

I determined that birds from a colony near the northernmost part of their range in Canada migrate to both the Pacific and Atlantic wintering sites known for this species.

The majority of birds tracked spent the winter in the waters of the Humboldt Current off the coast of Peru, while a small proportion of the birds spent the winter in the waters of the Benguela Current off the coast of South Africa and Namibia. I characterized the routes, timing, and distance of migration for Pacific wintering Sabine's gulls. Analysis of the movements of these individuals revealed that Sabine's gulls exploit highly localized areas of elevated marine productivity along a migration route of more than 28,000 km. I identified the Juan de Fuca Eddy off the southwest coast of Vancouver Island, British Columbia as a critically important foraging area during both north and southbound migration. This research also confirmed that some Sabine's gulls make a remarkable overland spring migration crossing multiple mountain ranges between the Pacific Ocean and Hudson Bay or the Bering Sea en route to the breeding site in the Canadian High Arctic.

4.2 Conservation implications

Understanding a species migration pattern, such as timing of movements and the routes and stopover areas used may help predict or explain changes in population size or distribution. The research presented in this thesis unravels a few aspects of the ecology of Sabine's gulls that have implications for conservation and can be used to inform management strategies.

Migratory Connectivity

The strength of migratory connectivity has important conservation implications. For example, events that occur at the wintering site (e.g. habitat alteration) may affect the reproductive success and survival (Marra et al. 2011, Rockwell et al. 2012). These carry-over effects can occur at the individual level (Rockwell et al. 2012), or at the population level (Fraser et al. 2012, Macdonald et al. 2012), especially if a species is under strong migratory connectivity (e.g. individuals from a breeding population spend the winter together) (Norris & Taylor 2006, Webster & Marra 2005). Information about how populations are geographically linked throughout the year is lacking for many species of migratory birds (Marra et al. 2011), including Sabine's gulls (Day et al. 2001).

My research is the first to consider the degree of migratory connectivity within populations of Sabine's gulls breeding in the Nearctic. Sabine's gulls breeding in the central Canadian Arctic are under weaker migratory connectivity than birds in colonies that migrate entirely to the Pacific wintering site or exclusively to Atlantic wintering sites, and may therefore be slightly more buffered from potential threats that occur during the non-breeding season.

Critical Habitat Used During Migration

Although Sabine's gulls are not currently threatened in Canada, identifying the habitats used during the non-breeding season has been recognized as a research priority (Day et al. 2001). This research provides a detailed account of the wintering range for Sabine's gulls in the Pacific, showing they are highly dependent on a few localized areas

of high marine productivity throughout their annual cycle. My tracks demonstrated that Sabine's gulls use a restricted area of the Humboldt Current off the coast of Peru, as well as confirmed the use of the Benguela Current off the coasts of South Africa and Namibia in the Atlantic. These are the two major eastern boundary upwelling systems in the southern hemisphere, which are divided into four independent ecosystems: the northern Humboldt (Peru), the southern Humboldt (Chile), the northern Benguela (Namibia), and the southern Benguela (South Africa) (Moloney et al. 2005, Shannon et al. 2008). The Juan de Fuca Eddy and the northern Humboldt current region must be recognized as particularly important sites for Sabine's gulls and the main area of conservation concern outside the breeding season.

Environmental variability in these systems is significant, and productivity fluctuates on annual (El Niño Southern Oscillation events) and decadal (alternating cool and warm periods) time scales (Moloney et al. 2005, Shannon et al. 2008). In addition, intense exploitation of the dominant pelagic fish species affects the ecosystem at all trophic levels, and massive changes in fish populations are accompanied by changes in abundance and composition of zooplankton (Alheit & Niquen 2004, Cury 2000). Sabine's gulls depend on the ready availability of small fish and zooplankton in these areas, and populations are likely to be influenced by fluctuations in the abundance and distribution of prey within them.

My research identifies the Juan de Fuca Eddy as a critical stopover site for Sabine's gulls during both spring and fall migration. The continental shelf off the southwest coast of Vancouver Island is extremely productive and is known to provide foraging habitat for many species of seabirds, whales, and fish (Burger 2003). The

increasing industrialization of the Pacific Northwest has led to increases in shipping traffic, which poses a high risk of oil spills and other contamination (Burger 1993, Burger et al. 2002).

Commercial fisheries overlapping with critical habitats using by Sabine's gulls may also affect survival during the non-breeding season (Day et al. 2001), but it remains unclear whether such overlap could pose a threat (i.e. resource depletion or direct mortality) (Bertrand et al. 2012, Lebreton & Veran 2013, Tasker et al. 2000), or a benefit, through increased food supply from fishing discards (Tasker et al. 2000). Sabine's gulls are known to associate with fishing vessels during the non-breeding season (Duffy 1989, Valeiras 2003, Wahl & Heinemann 1979), and therefore they may encounter or even exploit favourable foraging opportunities during stopover periods within the Juan de Fuca Eddy, which may explain population increase in some parts of their breeding range (Day et al. 2001).

Flexibility in Migration Patterns

It is widely accepted that bird migration is flexible in time and space (Alerstam 2011, Sutherland 1998), and there are many examples of migratory birds species that show flexible routing (Gilg et al. 2013, Stanley et al. 2012), or timing (Conklin et al. 2013, Studds & Marra 2011) throughout their annual cycle. Variation in migration schedules and patterns may be driven by ecological interactions en route (Both 2010, Thorup et al. 2006), phenotypic plasticity (Balbontín et al. 2009, Schmaljohann et al. 2012), endogenous mechanisms (Berthold 2001), or a combination of the above, however the

degree of flexibility and mechanisms controlling the variation observed continues to be challenged (Knudsen et al. 2011). It is clear though, that examining the amount of flexibility in migration timing and routes is important for predicting species-specific responses to climate change (Both 2010, Stanley et al. 2012).

By examining the routes and timing of migration of Sabine's gulls that spend the non-breeding season in the Pacific, I was able to show flexibility in both migration patterns and scheduling. In the spring, Sabine's gulls showed relatively consistent migration timing, but variation in migration routes; for example, some individuals followed an overland path towards the breeding site instead of following the coast. This trend has been noted in other species (Stanley et al. 2012, Vardanis et al. 2011), and suggests timing may be under stronger endogenous control, while variation in local conditions may drive route flexibility. Variability was also seen in stopover sites used, where in the most extreme case, one individual bird flew almost non-stop from the wintering site to the Gulf of Alaska, skipping spring stopover areas that the majority of other tracked birds used. Although further study is needed to fully examine the variation in Sabine's gull migration, it is possible that individuals may be able to change their route in response to short-term conditions (food availability, wind speed or direction, ice extent), which will potentially allow the population to adapt to changing climate conditions or resource abundance.

Many variations in migration routes of both Pacific and Atlantic Sabine's gulls have been observed (Day et al. 2001, Lambert 1972). Stenhouse et al. (2012) showed variation in fall migration, with some birds heading east to Iceland and Ireland, while others moved into the central North Atlantic Ocean before heading east towards the

European coast. Another bird travelled around the southern tip of Greenland and up the western coast before heading back east towards the stopover site (Stenhouse et al. 2012). It is also likely that a portion of the Atlantic population follows the eastern coast of Canada and the U.S. south before crossing the Atlantic to the wintering site, as indicated by a number of sightings during fall migration (see Day et al. 2001, Lambert 1972).

4.3 Future research directions

Additional research is needed to determine the boundaries of occurrence of Pacific versus Atlantic wintering birds among Nearctic breeding sites. Tracking birds from more eastern as well as more western Canadian Arctic breeding colonies would enhance our understanding of a possible east-west migratory divide. Additional migration tracks from Sabine's gulls breeding at other sites in the Nearctic would also clarify the degree of migratory connectivity between Nearctic populations. Alternatively, stable isotopes could be used to infer wintering locations of breeding Sabine's gulls to determine migratory connectivity between stages of their annual cycle (Hobson 2005). Since Sabine's gulls undergo a complete moult in the spring before starting northbound migration (Grant 1997, Howell & Dunn 2007), isotopic ratios within feathers collected at breeding sites across the Nearctic would reflect the food webs where they were grown (Mehl et al. 2004, Rushing et al. 2014). Despite the low resolution of results (Hobson 1999), this method would obtain large samples and be relatively inexpensive compared to tracking individuals.

There continues to be major gaps in our understanding of the migration ecology of juvenile Sabine's gulls (Day et al. 2001). It is unknown what routes juvenile birds take after they leave their fledging territories, where they spend their first winter, and what they do during their first summer (Day et al. 2001). Sightings appear to indicate more inland birds and perhaps different routes, particularly in eastern North America (see ebird. http://www.ebird.org). Satellite tags should be deployed on fledgling Sabine's gulls to reveal these completely unknown movements. Geolocators could also be deployed, however Sabine's gulls are not known to return to their natal sites until they are two years old minimum (Davis et al., unpubl. data), and breeding is confirmed at three years old (Stenhouse et al. 2001), making recovery of the tags difficult.

My study also gives rise to a variety of ecological, behavioural and genetic questions about how the migration pathways of Sabine's gulls are determined. For example, how is migration direction (and ultimately navigation to one of the wintering sites) determined in Sabine's gulls? Is migratory direction inherent as in some Palearctic warblers (Berthold & Helbig 1992, Helbig 1996), or learned by following adults during their first migration as shown for some storks (Chernetsov et al. 2004) and cranes (Mueller et al. 2013)? It has been suggested that adults leave the breeding area earlier than juveniles in Sabine's gulls (Lambert 1972), which may eliminate the ability for juveniles to learn from adult migratory pathways, however more research is needed to confirm this difference in migration timing between adults and juveniles. If migration direction is genetic, what is the resulting behaviour of 'hybrid' offspring? Perhaps they display intermediate migration routes (as shown by Delmore:2014kd and Helbig 1991), to spend the non-breeding season half way between Pacific and Atlantic wintering sites, or

alternatively they use the same route as one parental group (also shown by Delmore & Irwin 2014). Since migration direction tendency has only been quantified at one Canadian Arctic Sabine's gull colony (Nasuravaalik Island) and my data shows mixed migratory behaviour in adults (and no juveniles have been studied), more data is needed from other colonies (east and west) and data from juvenile Sabine's gulls (particularly "hybrid" offspring) is needed in order to gain insights into the degree of inheritance and learning. Future studies on Sabine's gulls could track the migration of juveniles from hybrid nests (Pacific/Atlantic pairs), and compare migration patterns to entirely Pacific and Atlantic wintering pairs in order to gain insights into the degree of inheritance and learning.

Despite our widespread knowledge of migration patterns and evolutionary determinants in birds (Alerstam et al. 2003), orientation of Arctic migrants is still largely unknown (Alerstam 2001, Åkesson & Hedenström 2007). My study therefore contributes to the broader study of how migratory behaviour of high latitude species is determined.

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Appendix 1 – Details of Tag Effect Study

Methods

I assessed the effect of geolocators on Sabine's gulls by comparing return rate, return date, adult body mass change, nest success, and chick growth between tagged and control birds. I weighed birds during incubation at tag deployment and recovery (including mass of tag and bands), where greater mass loss among the tagged birds compared to control birds would indicate tag-related stress.

To assess return rate and return date, I conducted daily checks for all individually colour-marked Sabine's gulls present within the Nasaruvaalik Island study area, during the month of June (pre-incubation). The small size of the island and the restricted area in which Sabine's gulls forage and roost makes it likely that the majority of birds present on any given day were accounted for.

In 2011, I marked and monitored all Sabine's gull nests on Nasaruvaalik Island to determine nest success. Nests were checked daily after initiation to determine laying order, monitored through incubation to quantify predation, and checked daily once hatching began to determine hatch success (see Mallory et al. 2012 for detailed methods). I defined treatment nests as nests with either one or two geolocator tagged parents, and control nests as nests without geolocator tagged parents (all breeding birds in the study were marked with a metal band and a combination of coloured Darvic bands).

To determine chick growth, recently hatched chicks (day 0 or 1) were banded with a metal band and a unique combination of coloured Darvic bands. Chicks were weighed in a plastic cup using a 100 or 300 gram (± 1 g) Pesola spring scale as frequently as

possible (every 2-3 d). The mean chick weight was calculated for each brood, combining data over 2 day periods (e.g. age 0-1 d, 2-3 d, etc.). Chick growth rate was assessed during the linear growth phase of Sabine's gulls (age 4 – 14 d) (Kondratyev & Kondratyeva 1984). I calculated chick growth rates for treatment and control broods, plotting growth rate with a regression of the natural log of mean brood mass on age (day). I compared the slopes of the growth rates (mass) between treatments to determine significance (Le Fer et al. 2008).

Results

When I deployed the smaller 2.1 g LAT2900 tags in 2010/11 and 2011/12, I found no difference in the mean body mass change from geolocator deployment to recovery between tagged and untagged birds (deployment mass = 184.9 ± 13.1 g, recovery mass = 185.6 ± 13.4 g, $t_{23} = -0.30$, $p = 0.8$). However, when I deployed the larger 3.8 g LAT2500 tags in 2008/09, there was a significant decrease (-10.3 g) in mean body mass of tagged birds compared to untagged birds ($t_2 = 7.75$, $p < 0.05$).

Of 32 birds outfitted with geolocators for the first year, 29 returned to the breeding site the following year (91%), with birds first observed on 21 Jun ± 5.5 d. Of 29 breeding birds trapped but not outfitted with geolocators, 27 returned the following year (93%), with birds observed arriving on 21 Jun ± 8.8 d. There was no significant difference in either return rate ($\chi^2_1 = 0.12$, $p = 0.7$) or return date ($t_{43} = -0.13$, $p = 0.9$).

I tested the effect of tags on nest success (hatch rate) in 2011, and found no significant difference between treatment nests (tagged parents) and control nests (banded,

but not tagged parents) ($\chi^2_1 = 0.6$, $p = 0.4$). The control nests ($n = 10$) hatched 19 of 23 eggs laid (83%) and the geolocator nests ($n = 14$) hatched 25 of 34 eggs laid (74%). I observed six eggs that were cracked (possibly by the geolocator) during incubation, and three of the cracked eggs failed as a result (50%).

Chicks hatched from nests with geolocator parents ($n = 22$) had a lower growth rate (11.6 g/d) than chicks from nests with only banded parents ($n = 23$; 12.2 g/d), however the difference in growth rate between the treatments was not significant (ANCOVA, $p = 0.85$).

Literature Cited

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